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THE STRUCTURE AND DEVELOPMENT OF CORALLOBOTHRIUM

With Descriptions of Two New Fish Tapeworms

WITH FIVE PLATES

BY

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Contributions from the
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under the direction of Henry B. Ward
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INTRODUCTION

Representatives of the genus Corallobothrium from American fish have never been described. Marshall and Gilbert (1905) report two members of this genus taken from *Ameiurus melas* (black bullhead) caught in the lakes at Madison, Wisconsin. La Rue (1914) refers to an undescribed species of Corallobothrium encysted in the livers of *A. melas* and *A. nebulosus* (common bullhead) from the Illinois River. Ward (1918) noted the presence of a species of Corallobothrium in *Ictalurus punctatus* (channel-cat) at Milford, Nebraska. Aside from these incidental references, the American literature contains no information on this interesting group of fish tapeworms.

The acquaintance of the writer with these cestodes began during the summer of 1925 while a survey of the parasites of fish from the rivers and lakes in the upper Mississippi and Missouri basin was in progress (Essex and Hunter, 1926). At that time cestodes belonging to Corallobothrium were found in the following hosts: *Ameiurus melas, Leptops olivaris* (mud-cat), and *Ictalurus punctatus.*

At the suggestion of Dr. Henry B. Ward an intensive study was begun in the spring of 1926 on the species of Corallobothrium infesting *I. punctatus.* As the investigation progressed it came to assume three distinct phases: (1) taxonomy and morphology; (2) seasonal occurrence; (3) life-cycle. It was discovered that two new species of Corallobothrium were represented in my collections. These two species are described and named in the present paper. No work having been reported previously on the seasonal occurrence of any fish tapeworm in America, an effort was made to obtain all possible information on this phase of the problem. This study has shed some light on the biological relations between the parasites and their hosts. Up to this time only a few experimental investigations on the life-cycle of fish cestodes have been reported by European workers and none whatever by workers in America. Since such studies are of especial biological significance, and since complete information on the developmental history of fish parasites is of great assistance to fish culturists in their efforts to combat parasitic diseases among fish, all data that I have secured on this phase of the investigation are presented in this paper.

My most sincere thanks are extended to Professor Ward for his inspiration, guidance and helpful criticism in this work. I am deeply grateful for the use of the zoological laboratories of Rockford College which were made available to me, during the summer of 1926, through the

kindness of Dr. Ruth Marshall and the generosity of the college authorities. I also acknowledge here the invaluable assistance rendered by Dr. David H. Thompson of the Illinois Natural History Survey, who furnished me several shipments of catfish for examination. Thanks are also due Mr. R. E. Richardson for the identification of minnows and for a collection of parasites from *Ictalurus punctatus*, and to Dr. S. A. Forbes for the use of unpublished data on the food of *I. punctatus* collected by the Illinois Natural History Survey.

Material and Methods

The parasites were killed in corrosive sublimate, Bouin's solution and 4 per cent formol. The first two gave good results, but specimens killed in formol were difficult to stain. Ehrlich's or Delafield's hematoxylin was used for totos and sections. Counterstaining was done with eosin or orange G.

Collection of the adult cestodes offers no difficulties, but it is a long and tedious struggle to find the smallest larval forms. A method was developed whereby plerocercoids which measured only 0.25 mm long could be collected with a saving of time and effort. Briefly stated, the procedure is as follows: (1) large parasites and particles of debris are removed; (2) remainder of intestinal contents scraped into quart jar of water and shaken thoroughly; (3) the mass is strained through a small plankton net; (4) the plankton net placed under faucet, running water allowed to play on contents until all possible material is washed through the net; (5) the residue is turned into a watchglass and examined under a binocular. This method is equally successful in collecting small trematodes.

A rapid method of reconstruction was developed in connection with the work on these cestodes. A plate of glass one foot square was placed under the camera lucida. With a wax pencil the structure to be reconstructed from a given section was traced on the glass. With plasticene the tracings were modeled. The next section was then oriented according to guide lines and the required tracings made from it. By means of blocks of plasticene the structures modeled from the second, third, and later sections were placed according to scale above those previously modeled. When completed, the organs were represented in three dimensions and in their proper relation. This method was employed in making the models represented by figures 39 and 41.

THE GENUS CORALLOBOTHRIUM

The genus Corallobothrium was created by Fritsch in 1886 to accommodate a species of cestode from *Malapterurus electricus*, an electric catfish of Egypt. Because of the resemblance of the scolex to the structure of an Oculina-like coral, he named the parasite Corallobothrium and called the species *C. solidum*. It was his opinion that this genus represented a connecting link between the Bothriocephalan and Taenian cestodes. He gave the following diagnosis for the genus: "Caput bothrio uno terminali, fere plano, ovali lateribus attenuatis, superficie et margine crispo. Acetabula quattuor cruciatim posita, in bothrii medio profunde inserta. Collum nullum. Corpus articulatum, depressum, subaequale vel retrorsum angustatum. Organa genitalia typica, orificia marginalia involuta." Fritsch says that the form of the scolex recalls that of Caryophyllaeus, "nur ist die Sauggrube in ihrer ovalen nach beiden Seiten leicht vershmälerten Gestalt, viel regelmässiger gebildet"; that the acetabular suckers are entirely obscured by the folds of the scolex and are revealed only in sections. The suckers agree in structure and arrangement with those of Taenia; the character of the whole body is strikingly solid and strong.

No other species was referred to the genus Corallobothrium before the work of Riggenbach (1896), who described a cestode from *Pimelodus pati*, a siluroid of Paraguay. This parasite was designated as *Corallobothrium lobosum*. Fuhrmann (1916) redescribed this form and gave a short redescription of *C. solidum*. On the basis of the cortical arrangement of the testes and vitellaria he removed *C. lobosum* from the genus Corallobothrium and created for it a new genus, namely, Rudolphiella. Later Fuhrmann and Baer (1925) reduced Rudolphiella to synonomy, and placed *R. lobosa* in the genus Ephedrocephalus.

Braun (1895) accepts the genus Corallobothrium and to Fritsch's diagnosis adds that neither hooks nor spines are present; that excretory vessels have secondary openings in the proglottids; and that the hosts are tropical or subtropical bony-fish. La Rue (1914) adds to Braun's diagnosis that the folds and lappets of the scolex may enclose the suckers as in a corolla and that no rostellum is present. He omits the secondary openings of the excretory system, given by Braun, and gives the habitat as the intestinal tract of the Siluridae.

The validity of the genus Corallobothrium was never questioned until the appearance of two papers by Woodland (1925, 1925a) in which he proposes to delete such genera as Corallobothrium, Choanoscolex,

Acanthotaenia and Gangesia and make them synonyms of Proteocephalus because they were founded on scolex characteristics. This author regards such characters as of specific value only, and proposes that the various arrangements of the reproductive organs with reference to the inner longitudinal muscle sheath shall constitute the bases for the designation of genera. In Woodland's opinion the scolex characters are of secondary importance as compared to the structure of the proglottids. However, if the early development of the cestodes is accepted as a guide in determining the order of sequence which is followed in arriving at the adult organization, and if those structures which appear first in the development of the individual are considered as having arisen first in the phylogeny of the group, then the scolex must be acknowledged as one of the most fundamental structures of the adult organism. In the development of Taenia and related groups, the scolex and a more or less indifferent neck are the only adult structures found in the cysticercus, and from them arise all other adult organs. In the development of the two new species described in this paper the scolex is likewise the first adult structure to appear, being differentiated at the end of 10 to 12 days development. When considered from this point of view, there is certainly sufficient reason for attaching generic value to the character of the scolex. Fuhrmann (1916) doubtless recognized this when he created a separate genus for *Goezeella siluri* instead of referring it to the genus Monticellia; the only essential difference between the two genera being that the former possesses a scolex of the Corallobothrium type. Furthermore, the scolex has long been used by helminthologists as a generic character, and to discard it now would result in more confusion of the nomenclature than seems to be justified. A recent publication by Stiles and Hassell (1926) contains the following statement: "The genus Taenia, in its modern concept, can be subdivided into at least three groups to which either subgeneric or generic rank may be given (according to one's personal point of view in respect to generic values)." A key follows in which the genera Taenia, Hydatigera and Taeniarhynchus are separated entirely on the basis of the scolex while Taenia and Taeniarhynchus are separated on the nature of the rostellum alone.

Since the characters which constitute a genus are considered largely a matter of personal viewpoint, Woodland is hardly justified in deleting genera which have been accepted previously by the leading workers in helminthology because, from his point of view, he does not regard the characters on which those genera were founded as of generic value. Therefore, I have followed Braun, Fuhrmann and others in accepting the genus Corallobothrium and the two new species described in this paper have been referred to that genus.

Corallobothrium is closely related to the genus Proteocephalus. The internal organization of the two genera is very similar. The scolex, however, is so distinctive that species belonging to the two genera can be separated by an examination of the scolex alone. Another character by which the species of Corallobothrium, which I have studied, may be separated from those of Proteocephalus, is in the position of the vagina with reference to the cirrus-pouch. In *Corallobothrium giganteum* and *C. fimbriatum*, the vagina in successive segments varies and may be either anterior or posterior to the cirrus-pouch. The descriptions of *C. solidum* are silent on this point, but if this condition is true of it also, there exist two distinct points of difference, scolex and position of vagina, between the species of Corallobothrium and Proteocephalus. Regarding the latter La Rue (1914) makes the following statement: "In Proteocephalus the vagina is usually anterior to the cirrus-pouch although there are a few species in which it is regularly posterior." Thus in the species of Proteocephalus the position of the vagina with regard to the cirrus-pouch is constant, while in the species of Corallobothrium it is inconstant.

The genus Corallobothrium may be defined as follows: With characters of family. Scolex bears four suckers situated on anterior surface surrounded by many irregular folds and lappets of tissue. Rostellum, hooks and spines absent. Neck broad, short. Vagina inconstant in position, anterior or poster to cirrus-pouch. Habitat: In Siluridae. Type species: *Corallobothrium solidum* Fritsch.

CORALLOBOTHRIUM GIGANTEUM NOV. SPEC.

In life these cestodes are milky-white in color. The scolex is usually attached in the region of the duodenum and the proglottids of a mature specimen may extend almost to the posterior limit of the intestinal tract of the host. They are strongly contractile and may draw themselves up to less than half the fully extended length. The strobilization is indistinct except in the posterior portion of the chain. The body surface is excessively wrinkled in this species as is true of the whole genus. The proglottids are so firmly joined that considerable force is required to tear them apart. The proglottid number varies from 150 to 300 or more.

Among seventy-five adult individuals before fixation, 60 cm was the greatest length observed. After fixation the longest individual was 44 cm. The usual length of preserved specimens ranges between 15 and 30 cm. In the largest living individuals mature proglottids are about 3 mm long by 2.5 mm wide; ripe proglottids 4 to 8 mm long by 1 to 0.5 mm wide, according to contraction. In the largest fixed specimen (44 cm) which was not fully extended, immature proglottids were from 0.25 to 0.75 mm long by 5 mm wide to 1 mm long by 3.5mm wide; mature proglottids from 1 mm long by 3.5 wide to 2 mm long by 2.25 mm wide; ripe proglottids

from 2 mm long by 2.25 mm wide to 5 mm long by 1 mm wide. In an alcoholic specimen 22 cm long, containing about 225 proglottids, 3 cm from the scolex, the proglottids are about 0.25 mm long by 2.5 to 2.75 mm wide; about 8 cm from the scolex they are 1 to 1.3 mm long by 2 to 1.5 mm wide; the last 20 proglottids measure from 1.5 to 2 mm long by 1 to 0.5 mm wide. In four toto preparations of sexually mature specimens which measure from 5 to 15 cm in length, immature proglottids are 0.10 to 0.84 mm long by 1.51 to 3.10 mm wide; mature proglottids 1 to 2.2 mm long by 1.3 to 1.89 mm wide; ripe proglottids 1.53 to 3.46 mm long by 0.73 to 1.15 mm wide. The segments in the anterior portion are always wider than long, but proceeding posteriad the length gradually increases at the expense of the width and the posterior proglottids of the chain are much longer than wide, the ratio begin from 2:1 to 8:1 (Figs 6, 26). The shape of the cestode in toto recalls that of a whip.

The form of the scolex is highly variable owing to different states of contraction. It may be globose (Fig. 15), quasi-conical (Fig. 5), quadrate (Fig. 2), or it may in a measure resemble the head of *C. fimbriatum* (Figs. 10, 11). In living specimens it varies from 1 to 2.75 mm in diameter. In six alcholic specimens, which are representative of the adult worms, the scolex measures from 1 to 2.16 mm wide. The ratio of the width to the length varies from about 1:1 to 2:1. Among four toto mounts the diameter is 1.47 to 1.68 mm and the length is 0.9 to 1.5 mm. The dorso-ventral dimension is usually slightly less than the transverse diameter. The four strongly muscular suckers, which are directed anteriorly, are largely concealed beneath a heavy fold of the cortex. From this fold project a large number of ridges and a few finger-like processes. The folds and lappets are much less pronounced than those of *C. fimbriatum* and *C. solidum* (Figs. 5, 10, 15). At times the suckers are drawn in and covered entirely (Fig. 11). When this occurs the scolex is drawn back into the neck region (Fig. 10). This gives the anterior extremity a flattened appearance. When the scolex is fully extended, the anterior extremity is rounded and the bluntly pointed apex projects from the center (Fig. 5). There is no rostellum or rudiment of a fifth sucker revealed in five sets of frontal and one set of transverse sections.

The suckers, which measure from 0.45 to 0.59 mm wide and from 0.53 to 0.59 mm long, vary in shape according to their contraction. In some specimens they are nearly spherical while in others they are longer than wide. One series of frontal sections shows each pair lying with their inner margins touching in the posterior portions while the anterior portions are quite widely separated, each one making an angle of about 30 degrees with the longitudinal axis of the worm (Fig. 33). In another series of frontal sections, each pair of suckers is separated by a distance of about 0.10 mm and they are directed anteriorly so that their longi-

tudinal axes are parallel with that of the scolex (Fig. 37). The first series was made from a specimen that was fairly well extended, the second from one that was much more contracted. The width of the openings varies from 0.10 to 0.19 mm and the length of the cavity may be as much as 0.33 mm.

At the apex of the suckers, surrounding the inner half of the opening, is a massive set of muscle bands which pass from the margin of the opening on one side in a circular course to the opposite side of the opening. They form a semi-circle about the apex of the suckers. In transections they appear as shown in figure 18; in frontal sections they are about 0.20 mm in diameter and resemble knobs (Fig. 37). Woodland (1925a) has reported a similar structure for the suckers of *Marsypocephalus rectangulus*. This structure functions as a sphincter and, as Woodland has suggested, doubtless aids in prehension. It was noted, in dealing with the living *C. giganteum* that they were detached with great difficulty when the scolex of one fastened itself upon another individual.

Besides the sphincter, each sucker is encircled by a very compact band of muscle fibers 16μ thick at the center. These fibers may be divided into two groups: those which surround the sucker in the frontal, and those which surround it in the sagittal plane. Within this band appears a layer of muscle fibers about 0.30 mm thick in the center. These are much less compact in their arrangement and all of them extend from the periphery of the sucker to the lining of the cavity. Lining the cavity of the sucker is a layer of cuticula which measures from 3 to 4μ in thickness.

Anterior to the suckers there is a rhomboid of muscle fibers (Fig. 35) and from the margins of the suckers many muscle fibers proceed into the neck region (Fig. 37). Posterior to the rhomboid of muscle fibers is a transverse cross of fibers. At the level of the sphincter a set of fibers pass from one sucker to the next (Fig. 18). Transverse sections through the posterior portions of the suckers show two bundles of muscle fibers, one arising from each of the inner margins of the suckers. These bundles pass diagonally to a member of the opposite pair. In their course they cross each other near the median line to form an eight-rayed cross or star (Fig. 28).

The neck in one set of frontal sections is about 1.60 mm long and 1.36 mm wide. It is easily recognized in frontal sections but it is not evident in much contracted totos. There is frequently very little constriction immediately posterior to the scolex. Thus the diameter of the neck region, when a specimen is much contracted, may equal that of the scolex (Figs. 10, 16, 37).

The cuticula, which varies from 4 to 9μ in thickness, is composed of two layers. A thin, more deeply staining layer about 1μ thick, covers the surface. Beneath it is a thicker, less deeply staining stratum at the inner

margin of which is found the very thin basement membrane, less than 1μ thick. Beneath this is a layer of circular muscles about 3μ thick. There are longitudinal muscle fibers just below the circular muscles. The former are interwoven with the outer ends of the spindle-shaped subcuticular cells which form a phalanx beneath the subcuticular muscles. These cells constitute a layer about 0.03 mm thick. They possess large nuclei which vary in shape, some of them being spherical and others elliptical. Each cell is drawn out into a fine process which can be followed as far as the basement membrane.

In the strobila the inner longitudinal muscle sheath is exceptionally well developed. In mature proglottids it measures from 0.05 to 0.07 mm thick. The fibers are arranged in irregularly shaped bundles. Just within this layer appears a band of inner circular fibers. This band constitutes a stratum from 6 to 16μ thick, which encircles the medullary parenchyma. In immature segments transverse fibers are quite numerous. Passing through the medullary region, as many as 60 bands of dorso-ventral fibers were counted in a single section of a mature proglottid.

The nervous system consists of a ring and two nerve trunks. The former is situated in the median region of the scolex at the level of the apices of the suckers. In transections it has the form of a cross, the rays of which project between the suckers (Fig. 35). Its greatest diameter in adults is from 0.33 to 0.40 mm. Arising from the lateral portions of the ring two trunks, which measure from 35 to 40μ in diameter, pass off parallel to the ascending excretory vessel and follow a course between the dorsal and ventral pairs of suckers along the inner margin of the longitudinal muscle layer (Fig. 30). In the scolex and throughout the proglottids these nerve trunks maintain the same relation to the inner longitudinal muscle sheath, and their diameter varies but little at any point in the chain.

The excretory tubules are very prominent in sections of this species. Four principal tubules are easily seen in sections of proglottids which are immature. When the reproductive organs are fully developed the excretory system is so crowded that at times it is difficult to distinguish it clearly. The four main longitudinal trunks are located in the lateral regions of the medullary parenchyma roughly parallel to the longitudinal nerve trunk of each side, the descending lying nearer the center than the ascending vessels.

The ascending tubules, which measure from 12 to 18μ in diameter, lie only 5 to 15μ from the nerve trunk, both in the neck region and in the immature proglottids. In these regions they follow a straight course with only slight deviations. The descending tubules are much larger in the regions just named, as they measure from 24 to 40μ. Their course is much more tortuous and their position with reference to the nerve trunk is much less definite.

The structure of the ascending and descending trunks is very different. Transections of the former show a heavy wall of hyaline material about 1μ thick surrounded by what appears to be a single layer of muscle fibers. Also the parenchymal cells are compactly arranged about these tubules (Fig. 40). The descending trunks lack the hyaline wall and also the layer of muscle fibers, and they are surrounded by a less compact arrangement of the parenchymal cells.

In a larval specimen about 4 mm long, cut in transverse section, the ascending trunks arise 0.14 mm from the posterior end of the individual where they measure from 2 to 5μ in diameter. They are found in the lateral medullary parenchyma. As they proceed anteriorly they increase slightly, measuring 8 to 10μ at a point about 0.8 mm from the scolex. As they enter the scolex they measure about 8μ in diameter. Upon reaching the scolex they pass laterally between the suckers and the longitudinal muscle layer of the scolex, following the outer margins of the suckers until the anterior level of the latter is reached, when they proceed inward toward the median line where they follow a tortuous course between the suckers before uniting with the descending trunks.

Branches of the descending trunks are more numerous in the central region of the scolex. The apex is ramified with both ascending and descending branches, but about the bases of the suckers there occur numerous coils of the descending tubules. Upon reaching the neck region, the main vessels proceed laterally, the ascending running dorsal and the descending ventral to the nerve trunk. In the neck the ascending trunks measure about 0.02 mm, or twice the diameter of the ascending ones. Throughout the length of the individual there is little difference in the diameter of the descending tubules since they measure from 20 to 25μ in the posterior region. There are no cross trunks apparent between the vessels of the same or opposite sides in the parasites at this stage of development. Furthermore, they follow practically a straight course throughout. About 0.08 mm from the posterior end, the two descending trunks empty into an excretory bladder. Just below the point of union with the descending tubules, the bladder measures 20μ dorso-ventrally and 27μ transversely. It narrows posteriorly and empties through a small duct at the extreme posterior end of the individual.

Frontal sections were made of a strongly contracted individual, about 15 mm long, in which a large number of proglottids had been differentiated. Here the excretory system is much more highly developed than in the individual just discussed. The position of the ascending and descending trunks with reference to each other has been slightly altered. At this stage they are parallel in a horizontal plane, with the ascending trunk more lateral or nearer the longitudinal nerve on each side. The diameter of the ascending is less than that of the descending trunks throughout

their extent. Both are more or less coiled in this individual. With the differentiation of proglottids an addition to the descending system has occurred. At the posterior limit of each proglottid is found a cross-trunk which in many instances equals in diameter the descending tubules. Also a small duct, 8μ in diameter, arises near the confluence of the descending and cross trunks. This passes to the posterio-lateral margin of the proglottids and empties to the outside through a small duct and pore (Figs. 34, 38). These same features are found also in the fully mature segments, but owing to the pressure of the reproductive organs they are more difficult to distinguish. The excretory system of this species agrees in all essential features with the description of Riggenbach (1896) for *Ephedrocephalus lobosus* (=*Corallobothrium lobosum*).

A study of frontal sections of the scolex and strobila in an extended and contracted condition has lead me to the conclusion that this system has more than an excretory function. When the scolex and strobila are contracted, the vessels are greatly diminished (Figs. 16 and 38). When the opposite is the case, the vessels are much distended (Figs. 21 and 34). This suggests the probability that the excretory vessels aid in the extension of the scolex and strobila.

Reproductive Organs

A common genital sinus, which measures about 64μ in diameter, occurs on the lateral margin of the proglottid from one-quarter to one-half the proglottid length behind the anterior margin. The usual position is within the anterior one-quarter of the proglottid. It is irregularly alternate in successive segments. The cortical wall surrounding the sinus protrudes sufficiently to be seen with the naked eye in toto mounts. This constitutes a genital papilla. The character and arrangement of the reproductive organs, for the most part, is identical with that of the other Proteocephalids. Each sexual unit occurs within the inner longitudinal muscle sheath (Fig. 20).

The male system will be considered first. The testes vary considerably in shape. Some of them are almost spherical, others pear-shaped, but the majority are elliptical. They measure from 0.05 mm to 0.08 mm in length, and from 0.03 to 0.06 mm in diameter. The number present in a single proglottid is from 80 to 100. They lie in a continuous field between the vitelline glands, extending from the anterior margin of the proglottid posteriad to the level of the ovary. Between the vitelline glands and the uterus they occur in two or three layers, but dorsal to the uterus only a single layer is present. Vasa efferentia were not observed in any of the preparations. In many sections the vas deferens passed among the testes and often there appeared to be a connection between the walls of the two. This relation could not be established for a sufficient number to warrant the statement that such is the usual condition.

At the level of the cirrus the thin-walled vas deferens, which measures from 0.03 to 0.05 mm in diameter, forms a compact mass of 15 to 20 coils that almost completely fill the medullary space between the vitellaria and uterus and extend anteriad and posteriad from 0.25 to 0.33 mm. (Figs. 7, 26). In mature proglottids they are usually distended with spermatozoa. At the point of entrance into the cirrus-pouch the vas deferens ends abruptly and at this point the ductus ejaculatorius takes its origin. After describing two or three coils it passes into the cirrus. The duct at the point of entrance into the cirrus-pouch measures about 16μ. A short distance beyond its point of entrance it doubles in diameter. Upon entering the cirrus it narrows again. Its lumen varies from 8 to 12μ in diameter. Its structure is almost identical with that of the cirrus.

The cirrus-pouch is usually elongate-oval in shape when the cirrus is inverted, but its form varies when the cirrus is everted. Apparently the extent of protrusion of the cirrus affects the shape of the cirrus-pouch. It assumes a variety of forms in successive segments. Some appear wedge-shaped, while others recall the form of a gourd (Fig. 7, 26). When the cirrus is inverted, the pouch measures from 0.26 to 0.33 mm long by 0.09 to 0.13 mm in greatest diameter. The wall of the pouch is from 3 to 5μ in thickness and is composed of longitudinal muscle fibers. Between the wall of the pouch and the cirrus is a loose network of connective tissue fibers with scattered nuclei. Immediately surrounding the cirrus is a compact layer of cells about 8μ thick. Wagner (1917) in his description of *Proteocephalus torulosus* calls a group of cells similarly located, subcuticular cells. Benedict (1900) in his description of *P. filicollis* and *P. ambloplitis* designates them as gland cells.

When the cirrus is inverted it measures from 0.20 to 0.23 mm in length and about 0.02 mm in greatest diameter and about the same at its point of union with the ductus. It is roughly cone-shaped, the base of the cone being adjacent to the genital sinus. In transections the wall of the cirrus shows a series of closely applied folds which almost close the lumen. The inverted cirrus is lined with a cuticular layer that extends to the ductus. Surrounding this layer are found longitudinal and circular muscles. When completely everted the cirrus reaches a length of 0.5 mm. Its diameter just outside the genital sinus is about 0.1mm, while its distal portion has a diameter of about 0.05 mm (Fig. 17).

In the female system the vagina opens into the genital sinus beside the cirrus in the same horizontal plane. Frontal sections of two individuals showed that the vagina may be either anterior or posterior to the cirrus. In one individual the vagina opened anterior to the cirrus on the right side in 14 proglottids, and on the left side anterior to the cirrus, in 12 proglottids. It opened posterior to the cirrus on the right side in 10 proglottids and posterior to the cirrus on the left side also in 10 proglottids.

In another specimen the relation was as follows: anterior to cirrus, right side, 18; anterior to cirrus, left side, 20; posterior to cirrus, right side, 10; posterior to cirrus, left side, 13. In these two specimens there is a close approach to equality in the dextral and sinistral position, and antero-posterior relation of the vagina and cirrus. For a distance of about 0.10 mm from the sinus the diameter of the vagina may almost equal that of the cirrus, and like the latter has a lining of rather heavy cuticula. A sphincter vaginae is present but weakly developed. At the end of the distance just mentioned the vagina narrows, and from there to the seminal receptacle it measures from 11 to 24μ and its lumen varies from 6 to 20μ in diameter. The greater diameter is only reached when the vagina is distended with spermatozoa. Since the vaginal opening may lie either anterior or posterior to the opening of the cirrus, the course of the vagina will vary somewhat. From the level of the genital sinus it may pass anteriorly for a short distance before proceeding toward the median line, or it may run between the coils of the vas deferens in a direct course toward the median line of the segment. At the same time it is directed ventrad. It passes through the ventral region of the medullary cortex for a short distance, then turns dorsally and for the remainder of its course to the seminal receptacle, it lies above the uterus. It is found in this last position throughout about two-thirds of its length. Anterior to the ovarian commissure when the proglottid is much extended, and posterior to it in contracted segments, the vagina widens gradually for about 0.10 mm, then it narrows suddenly, giving rise to a pear-shaped seminal receptacle which equals the width of the vagina at its narrowest point and is about 0.04 mm at its widest portion (Fig. 23). Leading from this structure is a narrow duct, the lower vagina, which joins the oviduct. This portion may be straight (Fig. 23) or coiled (Fig. 39). The position of the duct is dependent upon the contraction of the proglottids. Aside from a cuticular lining for a short distance from the genital sinus, the wall of the vagina is composed of muscle fibers and measures from 3 to 5μ in thickness. Only longitudinal fibers were distinguished. Like the cirrus, it is surrounded by a layer of gland cells throughout its length.

The bi-lobed ovary lies in the posterior portion of the proglottids. In fully extended ripe proglottids it is H-shaped. The two wings are broad and bluntly rounded posterior to the commissure, but anterior to it they taper to a rather sharp point and measure from 0.86 to 1.32 mm in length. The width of the ovary at the level of the commissure is from 0.33 to 0.46 mm (Figs. 23, 26). In fully extended ripe proglottids the structure of the ovary has a latticed or corded appearance as it is made up of a network of thin-walled tubules which are interwoven with one another. In mature proglottids the lobes of the ovary are much shorter and more compact, measuring from 0.46 to 0.80 mm in length and from 0.75 to 1.06 mm in width at the level of the commissure (Fig. 26).

As revealed by sections, the two lobes lie just beneath the inner longitudinal muscles in the dorsal region of the medullary parenchyma but the commissure dips ventrally. Near the median line, it connects with the muscular oocapt which is spherical in shape and measures about 20μ in diameter. It is surrounded by a layer of gland cells about 4μ thick. From the oocapt in mature proglottids the oviduct usually changes direction three or four times before reaching the posterior margin of the segment where it turns laterad and dorsad. Near its lateral limit it empties into the ootype. The greatest diameter of the oviduct is about 24μ. The lower vagina joins the oviduct at its last bend before the ootype is reached (Fig. 39).

The ootype, which is about the same diameter as the oviduct, passes laterally and dorsally for a short distance and then proceeds anteriorly. Near the anterior level of the vitelline receptacle it empties into the uterine passage. The wall of the ootype is very similar to that of the oviduct. The only striking difference between the two structures is the presence of the shell gland about the former, some cells of which measure 48μ long by 16μ wide. The processes of these cells pass into the wall of the ootype.

The uterine passage, which leads from the ootype, measures about 16μ in diameter. After bending upon itself once or twice it passes dorsal to the vagina and empties into the uterus near the median line at a point near the middle of the proglottid.

In mature proglottids the uterus has a diameter equal to about half the proglottid width. It is separated from the vitellaria on each side and from the dorsal musculature by the testes. It extends from the anterior margin to near the level of the ovarian commissure. It opens to the exterior through two or three uterine pores near the ventral median line. In mature proglottids the uterus possesses from 10 to 15 lateral pouches (Fig. 26). Their beginnings are very distinct in immature proglottids. In fully extended, partially spent proglottids the lateral pouches are relatively greatly reduced, giving the uterus the character of a tube with irregular borders (Fig. 6).

The vitellaria form two columns of a diameter of 0.08 mm which extend from the anterior to the posterior margin of the proglottid. They crowd the longitudinal nerve trunks close to the inner muscle sheath. They are follicular in structure, the follicles emptying into a central tubule. Near the level of the ovarian commissure a duct 16μ in diameter leads inward from each side. The two unite anterior to the oocapt, forming a common vitelline duct which proceeds posteriorly for about 0.05 mm and then widens to form the vitelline reservoir, which is from 40 to 56μ long and from 28 to 36μ wide. From the reservoir a narrow duct leads into the ootype near its point of union with the oviduct (Fig. 39).

AMPHITYPY

Amphitypy, or complete organ reversal, occurs in the position of all the interovarian organs in successive segments. This condition is not correlated with the position of any of the other organs of the reproductive system. For example, the genital sinus may be on the left margin with the vagina anterior to the cirrus and with the interovarian organs disposed as shown in figure 39. In another segment the genital sinus will be on the right with the vagina posterior to the cirrus and the interovarian organs will be arranged the same as in the figure just cited, or they may be just the reverse. The following data were taken from seven successive segments cut in frontal section.

Genital sinus	Right	Right	Left	Right	Right	Left	Right
Vagina anterior to cirrus	+		+				
Vagina posterior to cirrus		+		+	+	+	+
Oviduct right	+	+	+		+		
Oviduct left				+		+	+
Seminal receptacle right				+		+	+
Seminal receptacle left	+	+	+		+		
Vitelline reservoir right	+	+	+		+		
Vitelline reservoir left				+		+	+

Amphitypy has been observed among the Trematoda by many investigators (Looss, 1902: 789) but I have not discovered any reference to such a condition among the Cestoda.

A description of the living eggs is given later in this paper consequently only the ova within the uteri of sectioned specimens are considered here. The outer egg covering is so variable in amount and so irregular in shape that it is difficult to distinguish in preserved material. The second membrane is spherical and measures from 14 to 19μ in diameter. This membrane is closely applied to the oncosphere which measures from 8 to 13μ in diameter. The eggs of this species are the smallest produced by any of the species of Corallobothrium thus far described.

Because of the tremendous difference in the length as compared with the other two species, the smaller number of testes, and the great difference in the egg measurements, besides the other distinct characters to be pointed out, I regard the parasite under consideration as a new species which I shall designate as *Corallobothrium giganteum*. This name was given not only because it is the largest species of its genus but also because it is one of the largest known cestodes infesting fresh-water fish.

	Max. length	Sucker sphincter	No. of testes	Second egg membrane	Size of oncosphere
C. solidum	4 cm.	absent	140 to 180	20 to 24μ	13 to 16μ
C. giganteum	44 cm.	present	80 to 100	14 to 19μ	8 to 13μ
C. fimbriatum	8 cm.	absent	100 to 125	28 to 36μ	16 to 24μ

Only a superficial examination is necessary to separate this species from *Corallobothrium solidum* or *C. fimbriatum*. Besides the points considered in the preceding comparison, *C. giganteum* is distinct from the other species in the character of the scolex (Figs. 5, 10, and 15), the size and shape of the proglottids, shape of the ovary, and in the less extensive development of the uterus. The measurements in the preceding comparison were made on preserved material.

CORALLOBOTHRIUM FIMBRIATUM NOV. SPEC.

This cestode is usually found in the anterior portion of the intestine of *Ictalurus punctatus*, *Leptops olivaris*, or *Ameiurus melas*. The length, when ripe proglottids are present, varies from 15 to 80 mm among preserved specimens. The maximum breadth reaches 2.6 mm. Living individuals frequently reach a length of 70 to 90 mm when well extended. The strobilization is very distinct and the segments are more easily detached than those of *C. giganteum*. The number of proglottids ranges from 40 to 90. They vary in shape and size according to the state of contraction and the body size of the individual. The following measurements in millimeters were taken from 6 prepared specimens:

Immature proglottids
length 0.09, 0.16, 0.41, 0.19, 0.53, 0.16, 0.31, 0.27, 0.21
breadth 0.78, 0.46, 2.40, 1.57, 1.89, 1.68, 1.36, 1.15, 0.56

Mature proglottids
length 1.00, 0.95, 1.05, 0.50, 0.63, 0.73, 0.73, 0.63
breadth 1.9, 1.26, 1.36, 0.59, 1.26, 1.26, 2.60, 1.05

Ripe proglottids
length 1.05, 1.05, 1.01, 1.05, 1.00, 0.94, 1.05, 1.36, 1.36, 0.84
breadth 1.78, 2.60, 1.01, 1.01, 1.20, 1.36, 1.05, 0.73, 0.73, 0.84

The thickness varies from 0.5 to 0.7 mm. The immature and mature proglottids are almost invariably broader than long, while the ripe segments are longer than broad. In transections some ripe proglottids are flattened dorsally but rounded ventrally; in others the reverse is true.

In the descriptions of *C. solidum*, with which this form agrees very closely, that of Fuhrmann (1916) is the only one containing adequate measurements. He records the length of first proglottids as 0.09 mm; 5 mm behind the scolex as 0.23 mm and posterior segments as 0.65 mm. He gives the same maximum length and breadth as did Fritsch (1886) since he used the latter's preparations. Janicki (1926) gives the maximum length as 60 mm and maximum breadth as 3.5 mm but fails to record any other measurements for the proglottids. I have been unable to find in any *C. fimbriatum* specimens the definite surface structure which Janicki describes and figures for *C. solidum*. He states, "Von den zwei

mir vorliegenden Exemplaren weist das grössere eine sehr eigentümliche Gestaltung der Körperobeflache auf, indem die Rindenschicht durch tiefe longitudinal wie transversal verlaufende Einkerbungen das Bild einer mosaikartigen Täfelung hervorruft." There are, to be sure, longitudinal and transverse grooves which are largely the result of contraction (Fig. 1), but they are never as regular in occurrence as Janicki indicates for *C. solidum*.

This species possesses the same type of scolex as *C. solidum* and *Goezeella siluri* Fuhrmann 1916. It measures from 1.26 to 3.75 mm in transverse diameter The latter measurement was found in only one case and then the scolex was completely expanded. Figure 4 represents the scolex in a more expanded condition. Among 15 individuals bearing ripe proglottids the scolex usually measured about 2 mm in transverse diameter. The dorso-ventral is always less than the transverse diameter. In one fully expanded scolex the former is 2.31 mm and the latter is 2.61 mm. It is evident that the scolex of this species is subject to such extremes that many individuals must be studied to establish the range in size. When fully expanded, the scolex appears as a disc surmounting the proglottids and is set off sharply from the neck. In some contracted specimens the scolex is not thus sharply set off (Fig 1). The collar-like structure which surrounds the suckers may be folded over them laterally and dorso-ventrally, thus concealing them from view. Extending from each of the suckers toward the periphery of the scolex are deep grooves which mark the limits of the folds just described. The anterior surface of the scolex thus frequently resembles that of *Ephedrocephalus lobosus* as figured by Riggenbach (1896, Pl. 8, fig. 23b). The apex may be protruded as shown in figure 22, or it may be invaginated as indicated by figure 19. A rostellum is lacking, and hooks of any kind are absent.

Four suckers are situated in the anterior surface of the scolex. Their form and size vary according to the state of contraction. The following measurements in millimeters were made on sectional material:

Length 0.36, 0.43, 0.41, 0.37, 0.37, 0.38, 0.33, 0.45, 0.33, 0.53
Diameter 0.56, 0.53, 0.51, 0.37, 0.41, 0.40, 0.41, 0.38, 0.43, 0.60
Diameter of opening 0.13, 0.19, 0.21, 0.06, 0.06, 0.06, 0.12, 0.18, 0.18, 0.23

The measurements which follow were taken from toto-mounts:

Length 0.30, 0.23, 0.23, 0.19, 0.26, 0.39, 0.51
Diameter 0.38, 0.26, 0.26, 0.23, 0.23, 0.53, 0.88
Diameter of opening 0.16, 0.09, 0.06, 0.11, 0.13, 0.13, 0.41

A description of the musculature of the scolex and its suckers is unnecessary, since there is no apparent difference in this regard between *C. fimbriatum* and *E. lobosus* as described by Riggenbach. The peculiar,

knob-like structure or sphincter found in the suckers of *C. giganteum* is wanting here. In the three descriptions of *C. solidum* the size of the suckers is not given. From Fritsch's figure which was drawn to scale, I estimated the length of the suckers as 0.6 mm and the width as the same.

A neck is present, but its dimensions are dependent upon the state of contraction and the size of the specimen. Among eight individuals the neck in three was longer than wide, but in five cases it was wider than long. In millimeters the necks measure as follows:

Length 0.46, 0.63, 0.46, 0.53, 0.72, 0.96, 1.05, 1.26
Breadth 0.33, 1.89, 0.36, 0.56, 0.86, 1.21, 1.57, 0.94

In his description of *C. solidum* Fritsch states, "Man erkennt ohne Schwierigkeit, dass die schmalen, ohne Vermittelung eines Halses dem Kopf angefügten Glieder, sehr bald geschlechtsreif werden." Fuhrmann, using the same preparations, reports a short neck, while Janicki states that no neck is present in the specimens examined by him.

The cuticula of this species varies from 5 to 9μ in thickness which corresponds very closely to that of *Corallobothrium giganteum*. It is divided into two layers, an inner which stains deeply with hematoxylin, and an outer layer which stains very little. Beneath the cuticula courses the very thin basement membrane (less than 1μ). The subcuticular musculature shows a variation from the usual condition since the longitudinal fibers, which are present in a single layer, lie closely applied to the basement membrane. The usual layer of circular fibers was not distinguishable. Beneath the muscle fibers just described occur the spindle-shaped subcuticular cells which constitute a layer about 0.03 mm thick. The cortical parenchyma is very loosely constructed. In some sections it reveals a network of rounded spaces which measure from 6 to 35μ.

The musculature of this form is highly developed, but less so than in *C. giganteum*. Separating the cortical and medullary parenchyma are found the inner longitudinal muscles which constitute a layer from 16 to 30μ thick. These fibers are arranged in irregularly shaped bundles, but the bundles are not grouped in layers (Fig. 27). In *C. solidum* both Fuhrmann and Janicki report that laterally the muscles are more highly developed. This is also the case in *C. fimbriatum*. In this species transverse bundles, within the longitudinal muscle layer, are very numerous in immature proglottids; but in mature segments they are crowded against the longitudinal bundles by the growth of the reproductive organs. Many dorso-ventral bundles are present between the pouches of the uterus and in the lateral margins of the medullary parenchyma.

The nervous system consists of a nerve ring situated in the apex of the scolex near the anterior level of the suckers. A nerve trunk which measures 0.03 mm in diameter arises from each side of the ganglion and

passes posteriad between the outer margins of the two pairs of suckers. These trunks extend throughout the strobila in the lateral margin of the medullary parenchyma close to the longitudinal muscle sheath, as in *C. giganteum* and most Proteocephalids.

The excretory system is highly developed, but less so than in *C.giganteum*. It represents the typical condition as there are two pairs of vessels, a dorsal or ascending pair, and a ventral or descending pair. The former are more lateral in position and are found throughout the strobila closely applied to the nerve trunks. Their course is much less tortuous than that of the descending vessels. No branches could be found issuing from them. In ripe proglottids they measure about 4μ in diameter, but proceeding anteriorly the diameter increases until in the neck region it may attain as much as 24μ. The structure of the wall of the ascending trunk is very similar to that described for *C. giganteum* (Fig. 40). Frequently in ripe proglottids the vitellaria surround the dorsal vessel and it might be mistaken for a longitudinal vitelline duct.

The descending trunks, as already mentioned, describe a tortuous course. Their position is less rigidly fixed than that of the ascending vessels, because of the crowding of the reproductive organs, but they are always found in the ventral medullary parenchyma proximal to the ascending vessels. Their diameter varies from 24 to 40μ. Their walls are much thinner than those of the ascending vessels. The cross commissure which connects the descending vessels and the small vessels leading to the exterior which have been described for *C. giganteum*, are wanting in *C. fimbriatum*. Likewise I have been unable to discover any such vessels as Janicki has described for *C. solidum*. He states: "Die Foramina secundaria gelangen im hinteren Teil der Proglottis auf der ventralen Seite zur Entwicklung und stehen vermittelst besonderer Zweiggefässen mit den zwischen den grossen Ventralstämmen sich ausspannenden und vielfach secundär anfgelösten Commissuren in Verbindung." At no point can I find any vessels passing beyond the inner ongitudinal muscle sheath. The behavior of the ascending and descending vessels in the scolex is almost identical with that already described for *C. giganteum*.

Reproductive Organs

The common gential sinus occurs irregularly alternate on the lateral margin of the proglottid, almost invariably within the anterior fourth of the segment. A genital papilla is lacking in this species. The character and arrangement of the reproductive organs is typically Proteocephalid, as all the sex organs are contained within the inner longitudinal muscle sheath.

In immature proglottids where the testes are not crowded upon themselves or upon other organs, they are typically spherical and measure from 0.02 to 0.04 mm in diameter. In the mature proglottids, their shape varies from spherical to elongate oval, the form being dependent on the degree of pressure to which they are subjected (Fig. 32). The spherical testes measure from 60 to 72μ in diameter while the others range from 64μ long by 48μ wide to 80μ long by 72μ wide. The number of testes present in mature proglottids ranges from 100 to 125. Before the uterus has undergone a great deal of development the testes occupy all the available space in the medullary parenchyma (Fig. 14), but as the uterus grows it crowds the testes dorsally and laterally (Fig. 31). In mature proglottids only a single layer is present dorsal to the uterus, and only two or three layers are usually found lateral to it. In ripe proglottids the testes are crowded out of the lateral portions of the medullary parenchyma by the uterus, which extends to the vitellaria on each side (Fig. 31). They are found between the uterine pouches and frequently in the ventral portion of the medullary parenchyma. In the fully ripe segments they have almost completely disappeared.

Vasa efferentia were not distinguishable in any of the preparations. The vas deferens which measures from 16 to 50μ in diameter is extremely well developed. Its coils, from 25 to 30 in number, extend from the mid-line of the segment to the cirrus-pouch (Fig. 14). In immature segments they occupy nearly the anterior fourth of the medullary parenchyma, but when the segments become mature they are forced dorsally or between the pouches of the uterus (Fig. 29). Spermatozoa are present in the vas deferens when the uterus is in a very early stage of development (Fig. 14), i.e., in proglottids which are otherwise immature. Upon reaching the cirrus-pouch the vas deferens passes over into the ductus ejaculatorius. In immature segments it proceeds to the cirrus without coiling but in mature and ripe proglottids it describes three or four coils before emptying into the cirrus. Its diameter, upon entering the cirrus-pouch is about 16μ, but it widens as it proceeds, and frequently it may reach a diameter of 30 to 40μ before emptying into the cirrus. As it enters the cirrus it narrows again to about 16μ in diameter.

When inverted, the cirrus measures from 0.13 mm long by 25μ wide to 0.19 mm long by 36μ wide. It is typically club-shaped, with the narrow end at the proximal portion of the cirrus-pouch. When everted the cirrus measures from 0.16 to 0.23 mm in length and from 40 to 44μ in greatest diameter. It tapers gradually from its proximal to its distal end, where it measures about 0.02 mm in diameter. A terminal dilatation is wanting (Fig. 36). The cirrus-pouch varies from elongate oval, when the cirrus is inverted, to gourd-shape, when the cirrus is everted. It measures from 0.17 to 0.24 mm in length and from 0.07 to 0.09 mm in greatest

diameter. None of the descriptions of *C. solidum* record the size of the cirrus inverted or everted. The cirrus-pouch according to Fuhrmann is pear-shaped and measures 0.5 mm long by 0.22 mm wide. Janicki makes no reference to the shape but reports the length as 0.34 mm. The structural details of the vas deferens, cirrus and cirrus-pouch do not vary from those described for *C. giganteum.*

As in *C. giganteum,* the vagina opens into the genital sinus beside the cirrus in a horizontal plane, and may be either anterior or posterior to the latter. Both the cirrus and vagina pass into the medullary parenchyma between the dorsal and ventral excretory vessels and ventral to the longitudinal nerve trunk.

From the genital sinus the vagina passes along the ventral margin of the medullary parenchyma for about one-fourth of the proglottids diameter; then it courses dorsally and posteriorly to the mid-line of the proglottid, which it follows to the level of the ovarian commissure (Fig. 29). The course of the lower vagina will be discussed presently.

A sphincter vaginae is absent, or only weakly developed. The first part of the vagina, or the portion that usually extends from the genital sinus to about the mid-line of the segment, measures from 11 to 16μ in diameter. Its walls are somewhat heavier than those of the succeeding portion. The second portion of the vagina is thin-walled, and frequently reaches 32μ in diameter, but in such cases it is distended with spermatozoa. This portion of the vagina functions as a receptacle for spermatozoa. A distinct seminal receptacle, such as is found in *C. giganteum* is not present. Fuhrmann states that a seminal receptacle is wanting in *C. solidum.* Near the level of the ovarian commissure the second portion of the vagina is greatly reduced in diameter, giving rise to the narrow, more muscular, lower vagina which measures from 8 to 12μ in diameter. It passes dorsal to the ovarian commissure and follows along the lateral margin of the shell gland. Near the posterior margin of the segment it empties into the oviduct (Fig. 41).

The bi-lobed ovary lies in the posterior portion of the proglottids midway between the dorsal and ventral longitudinal muscles. In some transections the ovary presses against the dorsal and ventral longitudinal muscles thus filling much of the medullary space in the posterior end of the segment. Its shape may be roughly omegoid (Fig. 9) or it may be pyramidal (Fig. 8). The contraction of the segment affects the shape very materially. When much contracted, each wing of the ovary shows several secondary lobes (Fig. 12), which are less evident when the segment is fully extended (Fig. 13). A commissure joins the inner anterior margins of the two wings of the ovary. The inner posterior margins pass around the shell gland and proceed toward the median line but do not join. From the shell gland the two wings extend laterally. The pos-

terior margin of each wing parallels the septum of the segment, but the anterior margin dips down gradually until near the vitellaria on each side the two margins meet in a rather acute angle. Figures 8, 9, 12 and 13 represent some of the variations in the shape of the ovary. In an expanded ripe segment 1.58 mm wide the ovary measures 0.79 mm in diameter and only 66μ at the point of greatest length. In an expanded mature segment 1 mm wide the ovary measures 0.56 mm wide and 0.01 mm through the region of greatest length.

The following measurements in millimeters were made on mature segments which were more or less contracted:

Width of segment: 1.15, 1.11, 1.19, 1.26, 1.26
Width of ovary: 0.45, 0.46, 0.53, 0.54, 0.53
Length of ovary: 0.22, 0.23, 0.24, 0.21, 0.23

These measurements indicate that the width of the ovary is a little less than half the proglottid diameter.

Near the median line, and on the ventral surface, the commissure empties into the oocapt which measures from 28 to 38μ in diameter and is surrounded by a layer of gland cells about 16μ thick (Fig. 29). Fuhrmann gives the diameter of the oocapt of *C. solidum* as 28μ. From the oocapt the oviduct, whose maximum diameter is about 24μ, proceeds along the lateral margin of the interovarian space. Just before reaching the intersegmental septum it changes direction and crosses the interovarian space. Near the opposite side it bends posteriad and dorsad. After receiving the lower vagina it passes along the posterior margin of the proglottid. Upon reaching the middle of the interovarian space it turns anteriorly. Near this point it receives the vitelline duct and empties immediately into the ootype (Fig. 41).

The ootype, which measures from 12 to 16μ in diameter, lies in the dorsal portion of the medullary parenchyma. It is surrounded by the shell gland which is highly developed and measures from 0.09 to 0.16 mm. in diameter (Fig. 32). From its connection with the oviduct the ootype continues anteriorly from 0.09 to 0.10 mm, then it empties into the uterine passage. The uterine passage is a very thin-walled tube measuring from 16 to 20μ in diameter. From the ootype it proceeds anteriorly and dorsally. After making several coils it empties into the uterus near the middle of the proglottid.

The uterus begins growth in the ventral region of the medullary parenchyma but as it develops takes up more and more space, until in the ripe proglottids it crowds the vitellaria, excretory vessels and longitudinal nerves at each side, and occupies all possible space (Figs. 25, 31). The testes, vas deferens and other organs are crowded between the uterine pouches or flattened against the longitudinal muscle layer. The ovary is frequently pressed against the posterior limit of the segment

to such an extent that it is distorted in shape and may be difficult to distinguish (Fig. 25). At this stage the proglottid is hardly more than an egg-sac. From the main uterine stem arise from 10 to 14 uterine pouches, each of which in turn produces from 2 to 5 secondary pouches (Figs. 29, 32). On the ventral surface of the ripe proglottids occur one or two uterine pores.

The vitellaria form two lateral columns which extend from the anterior to the posterior region of the segment. They are more dorsal than ventral in position. The ventral excretory vessels lie beneath them. Their transverse diameter, which is dependent on the amount of contraction, ranges from 0.06 to 0.19 mm. At the level of the ovary or near the posterior limit of the proglottid each column turns inward until it comes in contact with the wings of the ovary (Fig. 14). From these inward-directed portions arise two vitelline ducts, one from each side, which run ventrad and meet lateral to the oocapt, forming the common vitelline duct, this proceeds dorsally and empties into the oviduct near its union with the ootype. The diameter of the two ducts just mentioned depends on the presence of vitelline cells; when empty they are indistinguishable, but when they contain vitelline cells the lumen measures from 11 to 16μ. At the point where the lateral ducts empty into the common vitelline duct a diameter of 32μ is frequently attained. From this region to its union with the oviduct the common vitelline duct measures only from 16 to 24μ in diameter. A distinct vitelline reservoir, like that in *C. giganteum*, is lacking in this species (Fig. 41). The vitelline cells present in the ducts are ovoid in form and measure from 11 to 14μ through their long axes.

This species shows amphitypy, the same irregularity in the arrangement of the organs of the interovarian space as described for *C. giganteum*; that is, in successive segments a complete reversal occurs. This reversal is not correlated with the right or left position of the genital pore, nor with the position of the vagina with reference to the cirrus. The organs may be arranged as shown in figure 41 or they may be just the reverse. In five successive segments the arrangement of the organs as shown below was observed.

Genital Pore	Left	Left	Left	Right	Right
Vagina anterior		+	+		+
Vagina posterior	+			+	
Oviduct right			+	+	
Oviduct left	+	+			+
Vitelline duct right	+	+			+
Vitelline duct left			+	+	
Lower vagina right			+	+	
Lower vagina left	+	+			+

A description of the living egg of the species is given later. Only the interuterine eggs of prepared specimens will be considered here. The outer membrane, which is so prominent just after the eggs have been discharged into the water (Fig. 42), is very difficult to see in sectional material. The second membrane is clear and since it is rather heavy its size is not affected greatly by preservatives. Its form is not spherical but is somewhat longer than broad. Through the long axis it measures from 28 to 36μ, the average being about 34μ. The contained oncosphere measures from 16 to 24μ in diameter, the average being about 20μ.

The eggs of this species are larger than those of *C. giganteum*. Fuhrmann reports the eggs of *C. solidum* as being small; "die Oncosphaere hat einen Durchmesser von 0.013 to 0.016 mm, die äussere Schale einen solchen von 0.020 to 0.024 mm" Janicki remarks: "Die reifen Eier von *C. solidum* sind ausserordentlich klein, sie messen nur 0.020 mm im Durchmesser, erscheinen aber sehr charakteristisch, so dass sie nicht leicht mit Eiern eines anderen Cestoden verwechselt werden können."

The foregoing description indicates that *C. fimbriatum* bears a close resemblance to *C. solidum*, but the following comparison shows some very outstanding differences between the two forms.

	Foramina secundaria	No. testes	Size of second egg membrane	Size of oncosphere
C. solidum	Present	140 to 180	20 to 24μ	13 to 16μ
C. fimbriatum	Absent	100 to 125	28 to 36μ	16 to 24μ

A lack of specific information on a great many points in the descriptions of *C. solidum* prevents a more complete comparison. The above data, however, are sufficient to mark the cestode under consideration as distinct from *C. solidum*. It is therefore regarded as a new species, which is designated as *Corallobothrium fimbriatum* because of the fringed character of the scolex.

DISTRIBUTION, ABUNDANCE AND SEASONAL OCCURRENCE

Corallobothrium giganteum and *C. fimbriatum* have been found associated in the intestinal tract of *Ictalurus punctatus*, *Ameiurus melas* and *Leptops olivaris* taken from the Rock, Mississippi and Illinois rivers. An intensive study was made only of *I. punctatus* from the Rock River, 130 of that species being examined during 1926. Nearly 70 per cent showed infection with one or both species of Corallobothrium. The following table is confined to the data on the adult parasites.

TABLE I

OCCURRENCE OF ADULT CORALLOBOTHRIUM

Date	Host	Number Examined	Stream	Number *C. fimbriatum*		Number *C. giganteum*	
				Present	Average	Present	Average
October, 1924	*A. melas*	3	Rock River	0	0	0	0
" "	*I. punctatus*	5	" "	0	0	0	0
June, 1925	*I. punctatus*	8	" "	16	2	21	2.6
" "	*I. punctatus*	1	Mississippi R.	10	10	8	8
July, 1925	*L. olivaris*	1	" "	1	1	1	1
December, 1926	*A. melas*	2	Illinois River	0	0	0	0
November, 1927	*A. melas*	5	" "	0	0	0	0
April, 1926	*I. punctatus*	14	Rock River	0	0	0	0
June, "	" "	10	" "	25	2.5	15	1.5
July, "	" "	46	" "	42	0.95	61	1.3
August, "	" "	25	" "	12	0.48	6	0.24
September, "	" "	6	" "	0	0	4	0.66
November, "	" "	11	" "	0	0	0	0
December, "	" "	18	" "	0	0	0	0

It is evident from the preceeding data that the adult form of Corallobothrium appears in the late spring or early summer, reaches its maximum during June and July, and disappears entirely the latter part of October or the first part of November. Additional data on the seasonal occurence of *Corallobothrium giganteum* and *C. fimbriatum* have been secured by an examination of the parasites collected by Mr. R. E. Richardson of the Illinois Natural History Survey, in connection with his studies on the food of *Ictalurus punctatus*. Only the stomach and about 5 cm of the intestine of each fish were preserved for his investigation. From such a limited portion of the intestinal tract, at best, only a small per

cent of the parasites present in each fish could be secured. In all, 1252 individuals were examined. From 954 *I. punctatus*, which were collected from June to September, 35 showed the presence of either one or both species of Corallobothrium. Among 278 of the same species of fish, collected from October to May, no parasites were recorded. While to be sure, a much larger number was examined during the period from June to September nevertheless a sufficient number was studied throughout the months from October to May to warrant the expectation of a proportionate percentage of parasitized fish, had the cestodes been present to the same degree during the whole year. Taken independently, these data would not be significant, but in connection with the evidence shown in Table 1 there can remain little doubt that the adult form of both species of Corallobothrium occurs only from spring to fall in *I. punctatus*.

Meggitt (1914) in his study of *Proteocephalus filicollis* states: "Almost every fish in autumn was infected with one or more of these parasites, 75 per cent of which were adult; in winter, the number of infected fish was considerably smaller, and adults were rare; while in spring, the proportion of adults again increased." He goes on to say that von Linstow failed to find adult *P. filicollis* at all in winter, and Zschokke noticed it only three times. Wagner (1917) makes the following statement regarding *P. torulosus*: "Wie verschiedene Autoren (Zschokke, v. Linstow, Kraemer, Riggenbach) übereinstimmend berichten, fällt die Reife der Geschlechtsprodukte der Fishtänien in Zeit zwischen Frühling und Herbst. Im Winter sind immer nur junge, noch nicht geschlechtsreife Tiere gefunden worden, was auch meine Erfahrungen an *I. torulosa* bestätigen." Thus my findings for Corallobothrium agree, for the most part, with those or *Proteocephalus filicollis* and *P. torulosus* as just quoted.

LIFE HISTORY OF CORALLOBOTHRIUM

Gruber, (1878) in his study of the copepods of Lake Constance, was the first to discover a larval cestode in the body cavity of a Cyclops. He found and described a procercoid from *C. brevicaudatus* and made the following conjecture: "Die Entwicklung zur Taenia erfährt der Wurm ohne Zweifel im Darme eines der zahlreichen Fische welche sich von den kleiner Krustern des Sees ernähren und es möchte wohl am wahrscheinlichsten sein, der Jungendzustand der *T. torulosa* ist, welche nach Rudolphi und Dujardin in Cyprinoiden unser Süsswasserseen lebt, obgleich es mir bis jetzt noch nicht gelungen ist, dieselbe aufzufinden." Following Gruber's discovery papers appeared by Mrazek, v. Linstow, and others, which described procercoids from Cyclops, Diaptomus, Gammarus and various ostracods. In many instances the larvae were identified with known adult parasites, but such studies usually admit of considerable doubt. Schmidt (1894) was the first to feed tapeworm eggs experimentally to the smaller aquatic crustacea. He succeeeded in infecting *Cypris ovata* with the eggs of the duck tapeworm, *Taenia anatina*, and described the development of the latter species from the oncosphere to the mature procercoid (Cysticerkoide).

Linton (1891) published a contribution to the life-history of *Dibothrium cordiceps* in which he says, "I have found a large Dibothrium in the white pelican (*Pelecanus erythrorhynchus*) which is evidently the adult form of *D. cordiceps*, of which the trout (*Salmo mykiss*) is the intermediate host." Linton gives no experimental evidence to substantiate his supposition. Consequently his conclusions are largely conjectural. No experimental work was done on the first intermediate hosts of fish cestodes until the work of Schneider (1903) who infected *Gammarus locusta* with the eggs of a species of Proteocephalus, Barbieri (1909) described a new cestode from *Alsosa finta* var. *lacustris* which he called *Ichthyotaenia agonis*. On insufficient evidence he gives the intermediate hosts for his cestode as Bythotrephes and Leptodora.

A successful study of the complete life-cycle of a fish cestode was made by Meggitt (1914), who traced the complete development of *Proteocephalus filicollis* by experimental methods. *Cyclops varius* was found to be the first and only intermediate host. *P. filicollis* is parasitic in the stickleback. The latter is infected by ingesting Cyclops which contain mature procercoids of *P. filicollis*.

Wagner (1917) made a splendid experimental study of the developmental cycle of *Proteocephalus torulosus*, for which he discovered *Cyclops strenuus* and *Diaptomus castor* as the first intermediate hosts. The fish

host, *Cyprinus orfus*, is infected with *P. torulosus* by feeding on copepods, some of which are infected.

Janicki and Rosen (1917) published the results of their successful study on the manner in which fish were infected with the plerocercoid of *Diphyllobothrium latum*.

Following this work, Rosen (1918) elucidated the life-history of two other species, viz., *Triaenophorus nodulosus* and *Abothrium infundibuliforme*. A year later the same worker outlined the development of *Ligula simplicissima*. It was found that the life-cycles of these forms were almost identical, excepting in *A. infundibuliforme*, the mature egg gives rise to a ciliated larva; the egg of that species, however, produces in the water an unciliated larva. In each case these larvae are eaten by some species of Cyclops and the subsequent development is practically the same. All of these cestodes except *A. infundibuliforme* require a second intermediate host, which is found among the young fish inhabiting the same waters. The adult host of *D. latum* is man, the dog, or possibly the cat; that of *T. nodulosus* and *A. infundibuliforme* is found among the fish, while that of *L. simplicissima* is some species of aquatic bird.

The literature contains no further studies on the life cycles of fish cestodes until the appearance of a fine paper by Kuczkowski (1925). This worker succeeded in infecting *Cyclops strenuus*, *C. serrulatus* and *C. oithonoides* experimentally with the eggs of *Proteocephalus percae* which is parasitic in *Gasterosteus aculeatus*, and likewise *C. strenuus* and *C. serrulatus* with the eggs of *P. longicollis* which is parasitic in *Coregonus albula*. In this study, Kuczkowski, gave particular attention to the development of the bladder appendage, or "cercomer," and its bearing on the "cercomer theory." Bangham (1925), in his studies of the cestode parasites of the black bass, reports that the procercoids of *P. pearsei* were found in a species of Cyclops and also in *Epischura lacustris*. Since no experimental work was done to establish the identity of the larvae there remains considerable doubt whether they were the procercoids of *P. pearsei* or some other Proteocephalid.

The papers just mentioned represent the work that has been done on the life-cycles of fish cestodes in Europe and America up to the present time. Therefore the study of the developmental history of fish cestodes from American hosts offers a nearly unexplored field. The investigation reported here was undertaken in the hope that some definite information might be obtained on the developmental cycle of the two species of American fish cestodes just described.

OBSERVATIONS CONCERNING THE EGGS

After the cestodes were removed from the intestine of the fish, they were washed immediately in tap water. This was done by grasping the

worm near the middle with a pair of forceps and rapidly raising and lowering it in the water. Each adult individual was then placed in a separate watchglass and covered with cold water. The excessive contractions of the worms caused the eggs to be ejected in milk-colored streams from the uterine pores of all the ripe proglottids. It was estimated that upward of a million eggs were emitted by an average-sized adult *Corallobothrium giganteum*, and one-half million or more by an adult *C. fimbriatum*. According to LaRue (1914) the eggs of the Proteocephalids usually have three membranes. The outermost membrane is thin, hyaline and spheroidal in form. The middle membrane is thick and granular. The innermost membrane is a clear, delicate but tough structure which is closely applied to the embryo.

The eggs of *Corallobothrium fimbriatum* are typically spherical, usually flattened and depressed at each pore. In their general outline they recall the form of an apple. The diameter varies from 0.08 to 0.14 mm. The outer membrane encloses a thick layer of transparent, gelatinous substance wich is responsible for the unusually large size of these eggs (Fig. 42). At the center of the gelatinous material is found a second membrane which is ovoidal in form, varying in size from 36 to 38μ by 30 to 32μ. The structure of this membrane is homogeneous and firm. It does not have a granular appearance in the living material nor in the eggs sectioned in the uterus. It presents rather the character of a chitinous covering which closely resembles, and is doubless homologous to, the shell of the Bothriocephalan egg. Meggitt (1914) reports an aperture in the second membrane of the eggs of *P. filicollis*. I have not observed such an opening in the eggs of either species of Corallobothrium. Lying beneath the second membrane of the eggs of *Corallobothrium fimbriatum* is a dense layer of granular substance about 0.10 mm thick. This material is doubtless composed of vitelline granules and other substances, either stored for the nourishment of the oncosphere or cast off during its formation. Surrounded by the granular layer just mentioned is found the six-hooked embryo. A third membrane could not be distinguished in either living or sectional material. The membranes of the living egg are so transparent that the oncosphere, which is about 20μ in diameter, can be seen distinctly. By a series of gliding movements it turns itself about within the shell or second membrane. Coincident with the movements of the body, the hooks are repeatedly extended and withdrawn. Observations made successively on the same individual for 12 hours showed that the oncosphere continued its apparent efforts to escape from its enclosing membranes. Its movements were rather spasmodic and intermittent. A period of vigorous contortions, during which it would frequently turn itself completely about, would be followed by a longer period of inactivity. On several occasions oncospheres were observed to work their way through

the granular layer and reach the shell, against which they repeatedly brought their hooks with all possible force but without apparent effect. The second membrane or shell seemed impervious to the action of the hooks. These observations indicated clearly that the oncospheres could not escape from the egg membranes by their own efforts.

Frequently in studying the eggs the rupture of the shell was noted. This permitted the escape of the oncosphere into the gelatinous covering (Figs. 43, 46). I could not always attribute the ruptured shell to the pressure of the coverglass. Meggitt (1914) who observed the same phenomenon in the eggs of *P. filicollis* offers the following explanation: "The cause of its [the oncosphere's] escape may be possibly due to osmosis, but it is more probable that it is due to the oncospheric movements." That is, the oncosphere forces its way out of the shell through the aperture which has already been mentioned. My observations on the structure of the shell and the activity of the oncosphere of *Corallobothrium fimbriatum* make the latter explanation untenable. When the oncosphere is found free in the gelatinous covering its structure and movements are more easily observed. The body of the oncosphere is covered by a very delicate membrane in which the proximal ends of the hooks are embedded. Within this membrane is the plasma, a grayish mass of homogeneous substance containing extremely fine granules. The plasma vividly recalls the color and structure of the protoplasm found in *Amoeba proteus*. Cell boundaries could not be distinguished, and it was quite impossible to detect the presence of any structures that might be interpreted as muscle fibers.

To determine the method by which the hooks of the oncosphere were brought into action, a long series of observations was necessary. The hooks are arranged in three pairs near the periphery of one pole of the embryo. Two pairs are placed laterally, while the third pair lies between. Usually the proximal ends of the hooks lie close together while the distal ends, bearing the hooks proper, are more widely separated. Before being thrust out the lateral pairs are brought up close to the middle pair. When this movement is completed the hooks of each pair are parallel with each other (Fig. 46). After watching their movements for hours, it became quite evident that the hooks were incapable of independent action; that their extension only occurred when the body of the oncosphere was elongated (Fig. 43); and that their return to a position of rest occurred only when the oncosphere again assumed a spherical form, i.e., the elongation of the oncosphere extended the hooks and its contraction withdrew them. The presence of muscle fibers attached to the hooks is extremely doubtful. My observations lead me to the conclusion reached by Janicki and Rosen (1917) in their study of *Diphyllobothrium latum*, viz., that the hooks, embedded in the membranous covering of the oncosphere, are brought into action as a result of the movements of the plasma rather than through the agency of muscle fibers.

In *Corallobothrium giganteum* only a glance at the eggs is needed to distinguish them from those of *C. fimbriatum* (Figs. 42, 50). The differences in shape and size are noticed at once. They are much smaller, measuring only from 30 to 60μ in diameter. Their shape is extremely irregular and varied. These differences are due largely to the distribution of the gelatinous material which surrounds the shell. It usually covers the shell in varying degrees of thickness, with here and there a finger-like projection which may give the egg a star shape. In some instances these projections are absent or less pronounced (Figs. 49, 50). The thickness of the gelatinous material is then more uniform (Fig. 49). The shell itself is almost a perfect sphere, measuring from 21 to 24μ in diameter, which is considerably smaller than that of *C. fimbriatum*. A layer of finely granular material is present within the shell, but its thickness is much less than in *C. fimbriatum*. The oncosphere, which ranges from 13 to 16μ in diameter, is not surrounded by a third membrane.

Although the structure of the eggs of the two species of Corallobothrium is identical, there is wide variation in the amount of the differentiated parts. Thus the ova of *C. giganteum* have less of the outer gelatinous substance, less of the granular material within the shell, and a much smaller oncosphere. Also, the shape and size of the egg as a whole, and the shape and size of the shell are quite different in the two species.

Experiments with the Eggs

To determine whether or not the eggs would hatch, watchglasses containing several thousand eggs were placed in the dark at room temperature. As a control another watchglass containing a like number of eggs was placed in the light at room temperature. Neither batch of eggs hatched. This experiment, together with observations on the structure of the eggs of each species, indicated that they did not give rise to free larvae but must be ingested in toto by the first host.

It was difficult to determine the viability of the eggs because of the action of bacteria. Thirty-six to forty-eight hours after the isolation of the ova myriads of bacteria began their destructive action upon them but feeding experiments with eggs which had been isolated for four days showed positive results. Eggs liberated in nature would very probably remain viable for a much longer period, since the bacteria should be less numerous in the open waters than under the restricted conditions in the watchglasses. In a medium containing a minimum number of bacteria it is probable that the ova remain viable for eight or ten days, and possibly for a longer period.

To ascertain the manner in which the eggs were disseminated—whether discharged from the proglottid before or after leaving the host—a series of observations were made on live fish. Adult *Ictalurus punctatus* were

placed in the laboratory aquaria, and for three or four successive days after their arrival the feces were examined once or twice a day. The feces were obtained by placing the fish on its back and firmly stroking the abdomen in the direction of the anus. The feces forced out in this way were inspected for the presence of cestode proglottids, eggs, etc. In such examinations of adult fish, eggs were present, but no detached proglottids were found. Furthermore, in post mortem examinations of over 100 adult *I. punctatus*, not a single detached ripe proglottid was recorded. From this evidence and that gained from the study of the adult worm (uterine pore, firmly attached proglottids, etc.), it is concluded that the eggs are forced through the uterine pores and pass out with the feces into the water, where they float about for a time and then sink to the bottom.

THE FIRST INTERMEDIATE HOST

In attacking the problem of the life-cycle of these parasites, two methods of approach were considered. First, it seemed reasonable to suppose that some clue to the intermediate hosts of the parasites might be gained by a thorough examination of the stomach and intestinal contents of the fish. Since the larvae of the cestodes probably must enter their final host passively with its food, a systematic study of the food of the fish was made a part of the routine of examinations. Secondly, the intermediate host might be discovered through direct experiment, i.e., by feeding ripe proglottids or eggs to any invertebrate animals which might possibly serve as the first intermediate host of the parasites.

The diet of 55 *Ictalurus punctatus* examined during the months of June and July consisted almost exclusively of crayfish, *Cambarus propinquus*, larval and adult *Hexagenia bilineata*, other insect larvae, and portions of mollusks and fish. The first two of these forms were considered as possible intermediate hosts, and macroscopical and microscopical examinations were made of the remains of those obtained from the stomachs of the fish, but with negative results. It was thought advisable, however, to attempt an infection by feeding them ripe proglottids or eggs.

Experiments with the crayfish, *Cambarus propinquus*, were carried on from July fifth to fourteenth. Crayfish secured from Rock River were placed in laboratory aquaria. After they had been allowed to fast for two or three days, living adult individuals of *C. giganteum* and *C. fimbriatum* were fed to them. Although they did not show a decided preference for the worms, they did eat them. At intervals varying from a few hours to a week after the worms had been ingested, the crayfish were examined. The intestine was removed, its contents teased out on a slide and inspected for the presence of oncospheres that might be in the lumen or for more advanced stages of the larvae encysted in the intestinal wall. Likewise, all the organs contained in the body-cavity were examined, and also the surrounding musculature. The results were negative.

Experiments with the Mayfly, *Hexagenia bilineata*, were made between July twentieth and August fifteenth. While the work with the crayfish was in progress, experiments were conducted on the larvae of *Hexagenia bilineata*. To obtain uninfected material adults were caught and stripped of their eggs, which were placed in large Petri dishes in the laboratory where they were allowed to stand. The water on them was changed every 24 to 48 hours. Seventeen days incubation produced hundreds of small larvae. Eggs of *C. giganteum* and *C. fimbriatum* were placed in two Petri dishes containing fifteen to twenty of these larvae and water-plant. Observations of the larvae under the binocular showed them swimming about or clinging to the vegetation in the containers. None of them seemed to be attracted to the tapeworm eggs. Subsequent examination of the larvae showed no trace of infection with the cestode larvae.

Experiments with *Cyclops albidus* also were conducted during July; these were coincident with the experiments just described. A supply of *Cyclops albidus* was collected from a lagoon near Rock River. A single individual was placed in each of six watchglasses, along with a spray of water-plant. After three or four days it was decided that they could live under such restricted conditions, as all of them were alive and very active. Then a drop of water containing the eggs of *Corallobothrium giganteum* was added to each of three watchglasses; and to each of the other three, a drop of water containing the eggs of *C. fimbriatum*. My observations of the Cyclops under the binocular convinced me that they were not attracted to the cestode eggs. They would, however, readily devour protozoa which were placed with them. On one occasion fork-tailed cercaria, obtained from a snail of the genus Physa, were placed in a watchglass with a *C. albidus*. To my great astonishment the Cyclops pounced upon one after another until fourteen were devoured.* Since efforts to observe the ingestion of the eggs by this species of Cyclops resulted negatively, and since no oncospheres or larvae were found when all of the individuals were afterward examined, it was concluded that further experiments with this species would be futile. It was evident that such a process of elimination applied to each animal which might be suspected of being an intermediate host of these cestodes, would consume much more time than I had at my disposal. Therefore, a more comprehensive method was conceived and pursued.

Mass infection of plankton was accordingly tried from July twentieth to August second. Not far from the Rockford College campus Rock River is obstructed by a dam. By holding a plankton net in the water that poured over this dam, it was possible in a few minutes to collect samples of a large number of the pelagic forms, as well as some bottom organisms that were

* This may account for the infrequency with which cercaria are met in plankton samples.

caught in the current and carried over the dam. A large quantity of the material gathered by this means was placed in each of two crystalizing dishes. Water-plant of the genus Cladophora taken from the face of the dam was placed in each dish. The bottom of one dish was strewn with the eggs of *Corallobothrium giganteum* and that of the other with the eggs of *C. fimbriatum*. Under these conditions all species were subjected to identical conditions; each was given an equal opportunity to ingest the eggs. It was hoped by an examination of the species contained in these cultures that the primary host of each worm might be discovered. After the cultures had stood for eight days, an examination of the different species present was begun. Since among the Copepoda a number of species had been discovered as the primary hosts of cestodes, representatives of that group were examined first. Each copepod was placed on a slide in a small drop of water, then excess water was drawn off with a fine pointed pipette so that only enough water was left to cover the specimen. This procedure minimized its movements and anchored it to the spot so that it could be examined successfully under the microscope. By this method several hundred copepods were examined.

From the culture in which *C. giganteum* eggs were placed, *Cyclops serrulatus* were found to be infected with from 1 to 6 larvae each, while *C. prasinus* were infected with from 1 to 3 each. From the culture inoculated with *C. fimbriatum* eggs, infected individuals were found among *C. bicuspidatus* and *C. serrulatus*, the former usually showing much heavier infection. No infection was observed among the copepods, *C. albidus*, *C. fuscus*, *C. bicolor*, or Diaptomus, nor among the Cladocera examined.

Since these results were accepted as a clear indication of the true first intermediate hosts of *Corallobothrium giganteum* and *C. fimbriatum*, further group infections were discontinued and a series of experiments were carried on with isolated groups of the species that had shown infection under mass conditions.

To determine the species and to prevent the inclusion in the experimental groups of individuals infected in nature each Cyclops was examined microscopically. Because of the transparency of the Cyclops, a cestode larva, when present, could be detected without great difficulty. The uninfected *C. serrulatus* and *C. prasinus* were placed together, and uninfected *C. bicuspidatus* and *C. serrulatus* were also allowed to occupy the same container.

Experimental infection of Cyclops was successfully attempted in August. These copepods were placed in a fingerbowl of tap water to which were added a few sprays of water-plant that had previously been rinsed thoroughly to reduce the protozoa in the fingerbowls as much as possible and likewise to prevent the entrance of uninspected Cyclops. On August twentieth at 11:30 A.M. the eggs of *C. fimbriatum* were placed in with

them. Oncospheres were found at 3:45 P.M. of the same day in the body-cavity of the Cyclops examined. Thus in a little more than four hours the oncospheres had migrated from the intestine into the body-cavity.

To determine whether or not the ingestion of the tapeworm eggs was selective or accidental, a study of the feeding habits of the Cyclops was undertaken. A fingerbowl containing *C. bicuspidatus* and *C. serrulatus* and the eggs of *Corallobothrium fimbriatum* was observed under the binocular. It was noted that the Cyclops foraged over the sprays of water-plant in the bottom of the fingerbowl and browsed on the particles of debris adhering to the vegetation and to the bottom. Any of the smaller protozoa which came near were instantly consumed. The outer gelatinous portion of the tapeworm eggs was repeatedly trimmed off and eaten, while the inner membrane (shell) containing the oncosphere was rejected. By continuous observation it was revealed that occasionally the inner portion also was taken in with the rest, which indicated that the eggs were eaten only incidentally, along with other organic material on which the Cyclops fed. This condition is in striking contrast with that of *Diphyllobothrium latum* and related forms in which the eggs give rise to ciliated larvae that successfully simulate protozoa and therefore constitute real objects of prey, attracting the Cyclops by their movements and tempting them to pursuit and capture.

The mass infection experiments had shown that *Cyclops serrulatus* could be infected by feeding the eggs of either species of Corallobothrium, but this point was not settled in respect to *Cyclops bicuspidatus* and *C. prasinus*. Therefore the eggs of *Corallobothrium giganteum* were fed to *Cyclops bicuspidatus* and those of *Corallobothrium fimbriatum* to *Cyclops prasinus*. The eggs of *Corallobothrium giganteum* were eaten by *Cyclops bicuspidatus* and the oncospheres migrated to the body-cavity, but no development was observed. The oncospheres, five days after the eggs were fed, measured only 16μ in diameter, their original size. The number present ranged from 2 to 15. This condition was noted in 15 different individuals examined from 1 to 5 days after feeding. The infection of *C. prasinus* with *Corallobothrium fimbriatum* larvae was light; only 2 individuals out of 10 harbored the larvae. The latter, however, were well developed.

Development of Corallobothrium fimbriatum *in Cyclops*

When *Cyclops bicuspidatus* and *C. serrulatus* had been identified as the first intermediate hosts of *Corallobothrium fimbriatum*, a study of the successive developmental stages in these copepods was begun. All observations were made on living material and within the period from August twentieth to September fourth. Beginning from one to four hours after feeding, the progress of development was traced through all of the stages found in these animals. As has already been stated, oncospheres were

first observed in the body-cavity of the Cyclops about four hours after the eggs had been placed in the watchglasses. Immediately following their liberation in the intestine of the Cyclops, the oncospheres increased slightly in diameter. While contained in the egg membranes, they measured from 16 to 20μ, but after liberation they measured from 18 to 23μ in diameter. Those present in the body-cavity about four hours after the eggs were fed measured from 20 to 25μ. Their form, however, constantly changed. They did not remain fixed to the intestinal wall of the host by means of their hooks but kept up almost constant motion. Since the elongation and contraction of the body put the hooks in operation, the action of the oncospheres resulted in the repeated extension and withdrawal of their hooks.

After the oncosphere had gained the body-cavity of the Cyclops, development proceeded very rapidly. Twenty-four hours after the eggs had been fed, four oncospheres were liberated, these measured from 30 to 40μ according to the stage of contraction. Figure 53 shows one as it appeared within the abdomen of the Cyclops, while figures 44 and 45 represent their condition 5 to 10 minutes after being liberated. Clear spherical bodies (cells) surrounded by heavy granules were seen throughout the body mass. When first liberated the oncospheres moved about with a gliding movement. During this time the hooks were kept in almost constant motion. Five or ten minutes after the larvae had been removed from the Cyclops indications of degeneration were seen. Then a transparent membrane was pushed out from the body of the oncosphere (Figs. 44, 45). In the individual represented in figure 45 there was a secondary membrane within the outer one from which the parenchyma had withdrawn. Thus it appears that the larvae at this stage possess two membranes; the outer may be considered cuticular while the inner may represent the basement membrane.

Seventy-two hours after feeding, the larvae ranged from 25 to 70μ in diameter (Figs. 55, 48). They were capable of distinct contractions which could be witnessed while they were still within the host. Upon removal, which was accomplished by tearing the Cyclops open by means of two sharply pointed needles, they appeared as a thin-walled sac containing globular bodies representing the parenchymatous tissue, which resembled an emulsion. Their movements were extremely feeble and continued for only a few minutes, then a spherical form was assumed and degeneration soon followed. The hooks, which were widely separated at one pole of the body at this stage, were incapable of effective action.

Four days after feeding, 12 oncospheres, measuring from 25μ in diameter to 135μ in length by 60μ in width, were removed from the body-cavity of one Cyclops. Figure 54 represents the most highly developed individual. Its sac-like body showed considerable differentiation. A cuticular mem-

brane surrounded the body and beneath it the tissue had a striated appearance, due to the development of the subcuticular musculature. Large cells surrounded by more or less heavy granules were evident. A few small calcareous bodies were to be seen scattered here and there throughout the body mass.

On the fifth day a Cyclops was dissected and 14 larvae were present in the body-cavity. These were from 0.06 to 0.24 mm in length. Except for the increase in size, no marked difference between these and the four-day individuals was noted.

One Cyclops observed on the sixth day had 16 larvae in the body-cavity (Fig. 51). Some of these larvae showed an increase in size over those of the fifth day, since they measured from 0.22 to 0.4 mm in length, according to the state of contraction. Upon being liberated, they moved about more vigorously for several minutes. The narrower end, which bore the hooks, showed more activity than the broader portion. Further differentiation had occurred, as the pole at which the hooks appeared presented a striking contrast to the homogeneous structure of the remainder of the body. It had become extremely transparent. The granules which appeared in the remainder of the body were entirely absent in this portion. At the proximal limit of this transparent region, or about 0.04 mm from the extreme body limit, a slight constriction appeared. In some individuals the hooks were attached to this portion, but in others they occurred just beyond the constriction in the granular region of the body (Fig. 56). In a number of cases some of the hooks were present on both regions (Fig. 57).

After six days no further increase in the length of the larvae took place, but many changes in their structural aspects occurred in quick succession. Thus on the seventh day there were evidences of differentiation at the pole opposite that on which the hooks were found. On the eighth and ninth days the larvae showed three distinct regions marked by two constrictions; one delimited the transparent region, the other occurred about one-third of the body length from the pole opposite that which bore the hooks (Fig. 56). By the tenth day, outlines of the developing suckers could be seen in this portion of the body, which was, therefore, the potential scolex.

Larvae studied on the eleventh day after the Cyclops were fed showed the four suckers well developed and at the anterior extremity a distinct end-organ. The large globular cells of the scolex region had disappeared. In their place a reticulum of minute, rounded cells with an occasional muscle fiber had appeared. The calcareous bodies, 5 or 6 in number, were confined, with a very few exceptions, to the middle portion of the larva The transparent region, more distinctly separated from the middle portion, formed a bladder-like appendage or cercomer (Fig. 57).

The development on the twelfth and thirteenth days differed from that on the eleventh in the following respects: The scolex, which had been differentiated by the eleventh day, was invaginated; the number of calcareous bodies had increased; and the length, by reason of the invaginated scolex, was somewhat reduced (Fig. 58).

Development in the Cyclops is completed by the fourteenth or fifteenth day after the ingestion of the eggs. The best indication of this is the invagination of the scolex and the loss of the bladder, or posterior appendage. Janicki and Rosen (1917) have given this larva the name of procercoid. After this stage is reached the parasite must enter another host before further development can be attained.

To indicate the extent of infection that may occur in such experimgnts, it should be stated here that from one culture 50 specimens of *C. bicuspi datus* were removed and 46 contained the larva of *Corallobothrium fimbriatum*.

Development of Corallobothrium giganteum *in Cyclops*

The development of this species corresponds closely with that of *Corallobothrium fimbriatum*. The oncospheres were observed in the body-cavity of *Cyclops serrulatus* eight hours after the eggs had been placed in the fingerbowls. Their presence was more difficult to detect because of their smaller size and greater transparency (Fig. 52). The number of larvae present in these species of Cyclops varied from 1 to 8. Therefore the infection was less intense than that found in the previous species where as many as 18 larvae were present.

No further observations on the progress of this species were recorded until the eighth day after the eggs were fed. By that time the larvae had attained a length of from 0.28 to 0.39 mm, which corresponded closely to the size of the larvae of *Corallobothrium fimbriatum* at the end of an equal period of time. However, the differentiation of various body regions had progressed considerably more than was true of the *C. fimbriatum* larvae in the same length of time. The suckers and end-organ were distinct and the bladder, or posterior appendage, was almost completely separated from the middle portion; and a larger number of calcareous bodies were present in this species than occurred in *C. fimbriatum* at a much later period. It was also noted that the globular cells, which were very prominent in *C. fimbriatum*, were much less pronounced in these larvae. Aside from the heavy granules scattered through the body, the structure was more homogeneous than that of the other species (Fig. 70).

On the twelfth day an examination of infected Cyclops revealed that the larvae had already become mature procercoids (Fig. 68). This was at least two days earlier than the same stage was reached by *C. fimbriatum*. The cuticula had increased greatly in thickness. The length of the larvae,

which was somewhat reduced by the invagination of the scolex, ranged from 0.2 to 0.25 mm according to the degree of contraction. As was true in the case of the other species, the bladder or posterior appendage had been shed and in addition a well-developed excretory vesicle had appeared in the posterior portion of the body. This organ, which measured from 5 to 9μ in diameter, could be traced anteriorly for about 0.06 mm when it became obscured by the surrounding structures. Efforts to detect smaller vessels, which doubtless emptied into it, failed entirely. The vesicle terminated posteriorly in a duct which emptied at the point where the bladder had been attached. Pulsations which began at the anterior portion and passed to the excretory pore, could be seen to proceed rhythmically along its length. An attempt to discover the vesicle in individuals that still possessed the bladder proved futile. There may be a relation between these two structures, besides one of sequence in development, but any statement further than this would be purely conjectural. Such a vesicle was not observed in *C. fimbriatum*. If present, it was obscured by other structures. It was easily seen in a later stage to be described presently.

Twelve-day larvae possessed a greater number of calcareous bodies, from 15 to 25. These were not restricted as in *C. fimbriatum* almost exclusively to the middle body region but were distributed everywhere along the periphery. More of them, however, were present in the posterior portion than elsewhere. The total number in this species is almost twice that discovered in any of the larvae of *C. fimbriatum* of about the same age (Figs. 58, 68).

The suckers and end-organ of the invaginated scolex could not be distinguished clearly in this species, as they were obscured by the overlying tissues. Following their liberation from the Cyclops, the larvae moved about actively for an hour or more. In one or two instances the scolex was evaginated. Figure 64 (*a* to *l*) represents the successive movements and shapes assumed by the larva before the evagination of the scolex. Figure 66 represents the appearance of one specimen with scolex everted after having been fixed and mounted. Maturity in the Cyclops has been reached by this species when the scolex has become invaginated, when the bladder appendage has been shed, and when the excretory vesicle has appeared.

It is interesting to note the difference in the rate of development found in these two species. Although *Corallobothrium giganteum* begins with a much smaller oncosphere, it develops at a rate sufficient to attain maturity in the Cyclops about two days before that point in development is reached by *C. fimbriatum*. Furthermore, the size of the adults in the two species would indicate that this difference manifests itself throughout the developmental cycle of each.

An interesting observation, which was the cause of considerable concern early in the course of these experiments, was made in connection with the

Cyclops that contained from 8 to 18 larvae. In such individuals several stages of development were frequently represented. For example, fifteen days after the eggs had been fed, mature procercoids and others, representing from three to ten days progress, were present in the same Cyclops. These differences were first considered to be due to the variability in the time at which the eggs had been ingested. The mature forms would thus represent the ingestion of the first eggs, and the less mature individuals the eggs eaten more recently. Further observation, however, indicated that this explanation was incorrect, since it was noted, by examination of the same Cyclops on successive days, that certain of the larvae increased very little in size. Among six *C. fimbriatum* larvae present in one *Cyclops serrulatus*, there were two fully mature, one represented the stage shown in figure 57, and three showed a development of about 10 days. In another Cyclops of the same species containing eight larvae of *C. giganteum*, three were mature (Fig. 68) and five were immature. Their movements after liberation were very feeble and lasted for only five or six minutes. One *Cyclops bicuspidatus* infected with 18 larvae of *Corallobothrium fimbriatum* showed nearly all the stages from the oncosphere to that represented in figure 56. This individual was examined just six days after the eggs were fed (Fig. 51). Many of the Cyclops examined from 25 to 30 days after the feeding of the eggs, showed this same condition of the larvae. This inhibition of growth among the larvae was probably due to the inability of the Cyclops to furnish sufficient nourishment for the complete development of more than three or four individuals.

In connection with the study of the development of *C. giganteum* an observation was made that caused considerable perplexity. In the body-cavity of several Cyclops, along with mature procercoids (Fig. 67), there frequently occurred as many or more very transparent, weakly contractile individuals devoid of hooks and calcareous bodies. They usually measured about 0.10 mm by 0.05 mm (Fig. 63), though one individual measured 0.30 mm by 0.10 mm. This individual was constricted near the middle and presented the appearance shown in figure 61. Kuczkowski (1925) in his study of *I. percae* reports the observation of forms similar to those I have encountered in connection with *C. giganteum*. He offers the suggestion that they represent the cast-off bladders (cercomers) of the mature procercoids. I am inclined to the same conclusion since the size of these transparent individuals is usually about the same as the bladder appendage. Furthermore, the structure of the two is almost identical. In a few instances, however, these peculiar forms were more than twice the size of the attached bladder (Fig. 61). Consequently, if they are accepted as being the bladders that have been separated from the mature procercoids, there must be claimed for them a certain power of independent growth.

A shifting of polarity was noted in the course of the development of the larvae of both species of Corallobothrium. During their early phases (from the oncosphere to about ten days), when removed from the Cyclops they moved slowly about with the end bearing the hooks directed anteriorly. Coincident with the differentiation of the scolex at the opposite pole, their polarity was reversed and movements thereafter were made with the scolex-end in advance. This phenomenon was noted also by Janicki and Rosen (1917) in their study of *Diphyllobothrium latum*.

The effects of infection on the Cyclops deserve brief consideration. Infection with a large number of oncospheres (20 to 50) appeared to cause the Cyclops no discomfort. Individuals so infected were quite as active as those unparasitized. Cyclops whose body-cavities contained from 1 to 6 larvae in advanced stages of development disclosed little evidence of any serious effects. When the infection went beyond this point, however, the Cyclops showed evidences of being greatly inconvenienced by the presence of the larvae. An infection as intense as is shown in figure 51 almost totally incapacitated the Cyclops. Such individuals no longer attempted to swim about but settled to the bottom of the fingerbowls and only moved when stimulated with the point of a needle or by vigorous stirring of the water. Then only a few strokes were made with the antennae and abdomen, after which they again settled to the bottom where they remained, apparently dispossessed of every desire for food or action. As has been pointed out by Meggitt (1914) and Janicki and Rosen (1917), such individuals fall an easy prey to the fish which feed on them. However, according to my observations no Cyclops that had been infected in nature contained more than a single procercoid. When it is considered that the chances of a multiple infection are rather slight in a large lake or river, the effect of the parasites on the Cyclops is of relatively little significance.

THE SECOND INTERMEDIATE HOST

The experiments in this line were carried on from August 24 to September 9, 1926. Studies on the food of *Ictalurus punctatus*, *Ameiurus melas* and *Leptops olivaris* had shown that minnows and occasionally other species of fish constituted a part of their diet. Copepods were never found in the food examinations of any of the foregoing species. Therefore it seemed improbable that such a high percentage of infection (nearly 70% in the case of *I. punctatus*) could have resulted from the accidental ingestion of infected Cyclops. Consequently no experiments were made on the direct infection of *I. punctatus* through the agency of the Cyclops. I inclined to the belief that infection of the catfish very likely occurred through the ingestion of forms that fed largely on the Entomostraca of the river. Since the Entamostraca were known to comprise a high percentage of the food of minnows, it was evident that some species of minnow might act

as a second intermediate host for the species of Corallobothrium. One of the most widely distributed minnows (*Notropis blennius*) was selected as the first subject. These fish could not be obtained except from the open waters of the streams in the vicinity of the laboratory. About 100 were taken from Rock River on August 24 and placed in the laboratory aquaria, where they remained 12 days before infection experiments were begun. During that time the weaker individuals were eliminated by death and the stronger were left for the experiments. No food was given them except bits of bread and cracker crumbs, on which they seemed to thrive very well.

From among these fish 8 individuals were examined but no larval cestodes were found. Although the findings which resulted from the examination of eight minnows are not considered as final evidence on the presence or absence of larvae in the remainder of the group, they may be taken as a fair index of the degree of infection in that particular school of minnows.

From a culture containing *Cyclops bicuspidatus* 30 to 40 specimens infected with procercoids were removed. These were placed in an aquarium (2′ long, 10″ wide, 12″ deep) containing water about three inches deep. Three of the smaller minnows were selected and placed in the same aquarium on September fourth. Three days later one minnow was examined and three cestode larvae were discovered on the mesentery along the outer wall of the intestine. Very probably there were others that escaped detection because of their extremely small size as they were only 0.2 to 0.4 mm in length, according to the exact degree of contraction (Fig. 60). The two remaining minnows were killed September ninth and preserved in formol for study by the section method.

Another group of three minnows was infected in the manner just described on September second. On the day of my departure from Rockford, September ninth, these minnows were placed in a quart jar containing 3 inches of water in which they remained for about 12 days. One of them died while I was enroute to Urbana. Of the two that remained one was killed October first, but there were no free larvae observed in the body-cavity. Any that may have been present had probably migrated to the musculature of the body-wall. The third individual was placed in an aquarium with a small uninfected *Ameiurus melas*. The aquarium overflowed shortly afterwards, and this gave the minnow an opportunity to escape. An examination of the catfish on April twenty-ninth gave negative results.

Sections prepared from a minnow killed three days after infection showed two larvae in the intestine, one outside of the intestine in the body-cavity, one in the ovary and three in the musculature. These larvae were not encysted (Figs. 65, 69). Since the larvae were found alive in the body-

cavity of the minnows and since a sectioned minnow showed their presence in the lumen of the intestine, in the coelomic cavity near the intestine and in the ovary and musculature of the body-wall, it is concluded that this minnow (*Notropis blennius*), and probably others, may serve as a second intermediate host for *Corallobothrium fimbriatum*. No experiments other than those already described were made on the life-cycle of *C. giganteum*. However, it is very probable that the developmental cycle of this species closely approximates that of *C. fimbriatum*.

After the conclusion of the experiments just described, I had an opportunity to secure additional data on the life-cycle of *Corallobothrium fimbriatum*. By the use of a specially devised trawl, Dr. David H. Thompson has been able to take small fish which are rarely obtained by the use of ordinary apparatus. In the early part of September, 1927, he secured 32 *Ictalurus punctatus* and shipped them to me alive. These fish measured from 2 to 3 inches in length. Six individuals out of the shipment harbored from 1 to 3 sexually mature *Corallobothrium fimbriatum*. The food of the young *I. punctatus* consists of plankton, insects, and various kinds of debris. It is quite improbable that infection with this cestode occurred in any other way than by the ingestion of copepods that harbored the procercoids. Therefore it was evident from my studies that the infection of catfish with *Corallobothrium fibriatum* might result either by feeding on minnows which harbored the larvae, or by the ingestion of infected copepods. The evidence for the latter contention seemed quite substantial but further experimentation was necessary to establish the former statement.

To determine whether or not infection with *Corallobothrium fimbriatum* might take place through the agency of a minnow, the following experiment was carried out. From the cestodes obtained from the small *Ictalurus punctatus* a large number of eggs were collected. These eggs were fed October third and fourth to uninfected *Cyclops prasinus*, and the procercoids developed in about 2 weeks. On October nineteenth the Cyclops were placed in an aquarium with two minnows (*Hybopsis storerianus*)* and I witnessed the ingestion of the Cyclops by the minnows. Two *Ameiurus melas* which had been kept in a laboratory aquarium since November 5, 1926, were used for the next phase of the experiment. No food had been given to these fish from June to September, 1927. Any parasites that they may have had when brought into the laboratory, it seemed reasonable to suppose had disappeared during their confinement. One of them was examined in September and no parasites of any kind were found. On October twenty-sixth the two minnows that had been fed the infected Cyclops were placed in the aquarium with the other *A. melas*. Both minnows were eaten. An examination of the catfish was made November eleventh and 6 larvae were recovered from the intestinal tract. They

* Identified by Dr. G. K. Noble, American Museum of Natural History.

measured about 0.3 mm in length. When the scolex was evaginated they resembled very closely the larva shown in figure 64*m*, but when the scolex was invaginated they resembled in every respect the procercoid of *Corallobothrium fimbriatum;* so much so that I have no doubt whatever as to their identity. The results of this investigation make possible an explanation of how adult catfish, which do not feed on plankton to any appreciable extent, become infected with Corallobothrium.

Plerocercoid Larvae

As has already been stated, the completion of the growth of the larvae in the Cyclops has been designated as the procercoid stage. Upon entering the next host transformation into the plerocercoid stage is begun. In Corallobothrium the first step in this process is the evagination of the scolex. Should the Cyclops infected with the procercoid be ingested by a catfish, development into the plerocercoid begins at once. However, should the procercoid be taken into another fish such as a minnow, which might be considered an accommodation host, the larva migrates from the intestine and takes refuge in the body-cavity or some organ of the second host where it remains until ingested by the definitive host. Little development occurs before it reaches the proper fish. There was close similarity between the larvae recovered from the minnow and the procercoid of *Corallobothrium fimbriatum* taken from the Cyclops. The only differences noted were the appearance of a larger number of calcareous bodies and an excretory bladder which was not observed in any of the procercoids when removed from the Cyclops (Fig. 60). The smallest plerocercoid found in the intestine of the catfish measured about 0.2 mm in length. In this individual, as in all the young plerocercoids, the scolex is the most prominent feature. The body is only a small cone-shaped projection in which no internal organs can be distinguished. Not until the larvae reach a length of about 1 mm is there a distinct resemblance to the adult individual (Fig. 62).

As has already been shown by Table I, no adult parasites belonging to the genus Corallobothrium were present among the fish examined from October to April. This was taken as decisive evidence that the adults do not appear before late spring or early summer and disappear entirely in the late fall or early winter. While this study was in progress it was discovered that the fate of the larvae was entirely different. Because of the difficulty of determining accurately the species of the smaller plerocercoids (Fig. 59), no attempt was made to record them according to species. It was found, however, that larvae of both species of Corallobothrium were present throughout the year. Therefore in the data recorded below, the total number of larvae present in each fish is recorded without regard to the species. In the examination of 130 *Ictalurus punctatus*, cestodes belong-

ing to any other genus than Corallobothrium were encountered only four times. In those instances the parasite belonged to the genus Proteocephalus. Since the larval stages of this form would be exceedingly rare, they should not affect very materially the data on the plerocercoids of Corallobothrium.

TABLE II

SEASONAL OCCURRENCE OF CORALLOBOTHRIUM PLEROCERCOIDS
Data from *Ictalurus punctatus* taken in Rock River

Date		Number Examined	Number Plerocercoids	Average per fish
April,	1926	14	6	0.43
June,	"	10	53	5.3
July,	"	46	150	3.2
August,	"	25	18	0.72
September,	"	6	2	0.33
November,	"	11	23	2.0
December,	"	18	49	3.3
	Total	130	301	2.3

These data indicate that the larvae which enter the fish host in the fall remain in the intestine through the winter. Since those found during December and April measured only from 0.5 to 0.8 mm in length, it is evident that little growth takes place during the winter and early spring. This cessation of growth may be due to temperature conditions or to the absence of sufficient nourishment for further development. Unpublished data collected by the Illinois Natural History Survey indicate that *Ictalurus punctatus* feeds very little during the winter. Doubtless both temperature and the lack of food are responsible for the inhibition of growth during this season.

COMPARISON OF PROTEOCEPHALUS AND CORALLOBOTHRIUM

With the exception of the work of Rosen, all of the experimental work on life-histories of fish cestodes has been on species of Proteocephalus (=Ichthyotaenia). Megitt's description of the development of *Proteocephalus filicollis* in *Cyclops varius* is incomplete in some respects. Briefly stated, he made the following observations: After the ingestion of eggs the oncosphere attaches itself to the wall of the alimentary canal where it remains about a week before breaking through into the body-cavity. After gaining the coelom it takes up a position near the anterior end of the carapace or in the head above the eye. The embryonic hooks gradually disappear. The body becomes covered with highly refractive bodies. The procercoid reached maturity at the end of three weeks. He states that the procercoid is an elongate gray body of variable size, without scolex or neck. The larva is devoid of divisions. Four suckers occur at the anterior end but an apical sucker is absent. The end bearing the suckers is never invaginated during development. No signs of excretory organs were seen.

The development of *Proteocephalus torulosus* in *Cyclops strenuus* and *Diaptomus castor* as described by Wagner is as follows: The oncospheres were observed in the coelom 24 hours after the eggs had been placed in with the copepods. At the end of 48 to 72 hours the larvae measured 20 to 30μ. They had settled themselves on or near the intestine. After a short time the larvae began to elongate. At one pole the first trace of the suckers appeared. Circular and longitudinal muscle fibers appeared along with excretory ducts and large calcareous bodies. An invagination occurred at the posterior end which was eventually taken over by the excretory bladder. The procercoid attained a length of 0.5 to 1 mm. It possessed four suckers whose radial muscles were distinct. The scolex possessed neither hooks nor rostellum. It was not set off from the rest of the body. The body was extremely contractile. The cuticula is broken up in a cover of fine hairs and bristles. In some individuals the embryonic hooks were strewn over the posterior half of the body. The excretory system was plainly visible in its entirety and consisted of an excretory bladder and a dorsal and ventral vessel on each side. Wagner makes no mention of a bladder appendage or cercomer.

Kuczkowski's description of the development of *Proteocephalus percae* in *Cyclops strenuus* may next be summarized. In the course of a few days after the infection, the spherical larvae of a diameter of 35μ, were observed in the coelom of the Cyclops. This larva soon began to grow

and lose its spherical form. A vaculated region appeared within the body mass which the author interpreted as the "lacuna primitiva" of Grassi and Rovelli. At this stage the larva was 41 to 55μ in diameter. There was a decided growth in length and an increased contractility. A cercomer appeared from 14 to 21 days after the infection, then the length of the larva was from 138 to 327μ and the length of the bladder from 13 to 42μ. The bladder was without hooks. These were found on the posterior portion of the larval body. The procercoid possessed four elliptical suckers. No apical sucker was present but a bladder-like protrusion was noted at the apex of the scolex. The figures indicate that the cuticula was smooth. A well developed excretory system was present, also circular and longitudinal muscle fibers. The larva showed the typical calcareous bodies.

A comparison of the developmental phases of the species of Proteocephalus just described with those of Corallobothrium brings out some rather significant differences. In Proteocephalus the bladder appendage or cercomer is entirely wanting in two species according to the descriptions given and rather rudimentary in the third. In Corallobothrium the cercomer is a decidedly prominent structure whose length equals one-third that of the body, 40 to 60μ, and is never rudimentary. In *Proteocephalus percae* where the bladder has been observed, it shows signs of being rudimentary since in some cases it measures only 13μ in length. According to Kuczkowski the cercomer of *P. percae* never bears the embryonic hooks. These hooks are always found on the posterior portion of the body. This condition is likewise true of the other species of Proteocephalus which have been described. In Corallobothrium, however, they may be confined to the cercomer, divided between the cercomer and the body, or all on the body. In Proteocephalus the suckers are differentiated near the anterior end of the larval body without the scolex being set off. The scolex is never completely invaginated. In Corallobothrium the scolex is set off early from the the rest of the body (Figs. 57, 70) and soon afterward is completely invaginated. The Proteocephalus procercoid bears a close resemblance to the plerocercoid found in the intestine of the final host. This is not true of the procercoids of Corallobothrium, in which a decided transformation takes place in the procercoid before the plerocercoid stage is attained (Figs. 58, 59, 68). In every case the Proteocephalus procercoid has a greater length than that of the Corallobothrium procercoid. In the three species of Proteocephalus whose life-cycles have been studied, only one intermediate host is required. The evidence is fairly substantial that at least one species of Corallobothrium, *C. fimbriatum*, may use two intermediate hosts for its development. The striking differences in the development of these cestodes, combined with the differences in adult morphology, should be, in

my opinion, sufficient evidence to satisfy the most critical worker that Corallobothrium should remain a separate genus.

COMPARISON WITH *DIPHYLLOBOTHRIUM LATUM*

The species of Proteocephalus have been compared with those of Corallobothrium from the point of view of their development. A similar comparison between *Diphyllobothrium latum* and the species of Corallobothrium is of interest. As described by Janicki and Rosen, *D. latum* develops in the following manner: The ciliated larva is ingested by *Cyclops strenuus*. Within a few hours the oncosphere has gained the body-cavity of the Cyclops. The larva remains attached by its hooks to the wall of the intestine 10 to 15 days, during which time it loses its contractility. It becomes elongated and at the end of 6 to 8 days development measures 0.10 to 0.15 mm. At the end of from 8 to 12 days the larva shows calcareous bodies, longitudinal and transverse musculature and a strongly developed cuticular covering. On the twelfth day after beginning development the opposite poles of the body show differentiation. By the twelfth to fifteenth day a special bladder appendage with the embryonic hooks upon it is formed. Now the larva measures from 0.35 to 0.40 mm. At the end of 15 to 20 days the larva has attained a length of from 0.5 to 0.6 mm. Then the bladder gradually degenerates and disappears. At the time of the formation of the bladder an evagination occurs at the opposite end. Later this structure is capable of being invaginated. At the end of development in the Cyclops the larva is covered, especially its anterior portion, with bristle-like processes. At this stage the body is highly contractile. The scolex and excretory vesicle are not formed by the larva while in the Cyclops. These two organs make their appearance in the second intermediate host.

The behavior of the oncosphere of Corallobothrium in some particulars is decidedly different from that of *D. latum*. In the former the oncosphere does not remain attached to the intestine of the Cyclops by its hooks. The hooks may be seen in action at any time after the oncosphere has gained the body-cavity. Neither does the larva lose its contractility. The development of Corallobothrium larvae is much more rapid, as they attain their greatest length at the end of from 6 to 8 days. In *D. latum* the bladder bears the embryonic hooks; but in Corallobothrium the bladder may or may not possess the hooks. The scolex and excretory vesicle are not formed in *D. latum* until the larva has developed in the second intermediate host. In Corallobothrium the scolex is formed early, by the tenth or twelfth day. The species of the last-named genus do not possess the covering of bristle-like processess noted for *D. latum*. The Corallobothrium procercoid is never more than two-thirds the length of the procercoid of *D. latum*. Another interesting difference is found in the

appearance of the excretory vesicle. In *D. latum* this organ does not occur until the plerocercoid stage, but in *Corallobothrium giganteum* it arises during the development in the Cyclops. It was not observed in *Corallobothrium fimbriatum* until the plerocercoid stage. This might be expected since the procercoid development of *C. giganteum* covering 10 to 12 days is more rapid than that of *C. fimbriatum* which takes 14 to 15 days.

Janicki and Rosen never found more than one mature procercoid in the same Cyclops. I have observed as many as three mature procercoids and three individuals representing 10 days development in the same host. The largest number of larvae reported for *D. latum* in a single Cyclops was from 8 to 10. As many as 18 were found in a single host infected with the eggs of *Corallobothrium fimbriatum*.

This comparative study of the Bothriocephalid, Proteocephalus, and Corallobothrium procercoid furnishes evidence indicating an intermediate postition for Corallobothrium between the Bothriocephalids and the genus Proteocephalus. First, in the Bothriocephalids the cercomer is always present and nearly always bears the embryonic hooks, but in Proteocephalus it may be wanting entirely. When present, however, it never bears the embryonic hooks. In Corallobothrium the cercomer is always present and it may or may not possess the hooks. Second, the procercoid of the Bothriocephalids bears little resemblance to the plerocercoid, whereas the Proteocephalus procercoid is almost identical to the plerocercoid while the procercoid of Corallobothrium does not bear a close resemblance to the plerocercoid stage. The Bothriocephalids usually require two intermediate hosts, the Proteocephalids only one, while Corallobothrium may or may not use two intermediate hosts.

EARLY DEVELOPMENT IN BOTHRIOCEPHALIDS AND PROTEOCEPHALIDS

Observations on the early development of the Proteocephalids are in close agreement with those on *Diphyllobothrium latum*, *Triaenophorus nodulosus*, *Abothrium infundibuliforme* and *Ligula simplicissima*. There are, however, a number of differences that should be considered. The egg of the Proteocephalids when extruded from the uterus, possesses a gelatinous outer covering which enables it to float about for a time before sinking to the bottom of the stream or lake. Within this gelatinous material is found a second membrane (shell) which contains a quantity of granular material and the fully-formed oncosphere which may or may not be invested with a third membrane. The oncosphere of the Proteocephalids is held a prisoner within its membranes until liberated through the agency of the first intermediate host. The egg of each of the Bothriocephalids mentioned above, closely resembles that of the trematodes. A gelatinous covering is absent. The oncosphere may be fully developed before the egg

is extruded from the uterus, as in *Abothrium infundibuliforme;* or an incubation period of varying length may be necessary after the egg is extruded, as in *Diphyllobothrium latum*. When the egg is mature it is composed of an outer shell, which I consider to be homologous with the second membrane of the Proteocephalid egg, and a layer of cells which envelops the oncosphere. This layer of cells is probably homologous with the innermost membrane reported in most Proteocephalid eggs. Contrary to what occurs in the Proteocephalids, the egg of the Bothriocephalid hatches, thus liberating the oncosphere. The layer of cells enveloping the oncosphere may be provided with cilia, as in *D. latum*, or the cilia may be wanting, as in *A. infundibuliforme*.

A comparison of the size of the oncospheres of certain Bothriocephalids and Proteocephalids is given in the following parallel columns.

Bothriocephalids	Size in micra	Authority	Proteocephalids	Size in micra	Authority
Diphyllobothrium latum	22 to 30	Janicki and Rosen	*Proteocephalus filicollis*	27(estd)	Meggitt
Triaenophorus nodulosus	22 to 24	Rosen	*P. torulosus*	20 to 30	Wagner
Abothrium infundibuliforme	50 to 60	Rosen	*P. percae*	28 to 35	Kuczkowski
			Corallobothrium fimbriatum	20	Essex
			C. giganteum	13 to 16	"

It is of interest to note that the first intermediate hosts of the Proteocephalids and Bothriocephalids considered in this paper are found exclusively among the copepods. The species recorded in the following columns have been studied experimentally.

PROTEOCEPHALIDS

Parasite	First Intermediate Host	Authority
Proteocephalus filicollis	*Cyclops varius*	Meggitt
P. torulosus	*Diaptomus castor*	
	Cyclops strenuus	Wagner
P. percae	*Cyclops strenuus*	
	C. serrulatus	
	C. oithonoides	Kuczkowski
P. longicollis	*Cyclops strenuus*	
	C. serrulatus	Kuczkowski
Corallobothrium fimbriatum	*Cyclops bicuspidatus*	
	C. serrulatus	
	C. prasinus	Essex
C. giganteum	*Cyclops serrulatus*	
	C. prasinus	Essex

BOTHRIOCEPHALIDS

Parasite	First Intermediate Host	Authority
Diphyllobothrium latum	*Cyclops strenuus*	
	Diaptomus gracilis	Janicki and Rosen
Diphyllobothrium latum	*Diaptomus oregonensis*	Essex
Triaenophorus nodulosus	*Cyclops strenuus*	
	C. fimbriatus	Rosen
Abothrium infundibuliforme	*Cyclops strenuus*	
	C. serrulatus	Rosen
Ligula simplicissima	*Cyclops strenuus*	
	Diaptomus gracilis	Rosen

There may be some significance attached to the fact that *Cyclops strenuus* acts as the first intermediate host of all the Bothriocephalids and three of the Proteocephalids; that *Cyclops serrulatus* is found among the first intermediate hosts of both groups.

AFFINITIES OF THE PROTEOCEPHALIDS

A study of the life-cycle of organisms has long been used as a guide to their true affinities. Adult morphology alone is not always a reliable criterion of true relationship. Certain forms, the barnacles and ostracods for example, which were thought to be widely separated phylogenetically on the basis of the adult structure, have been brought close together through the discovery of their developmental cycles. The lack of complete knowledge on the life-cycles of the vast majority of the Cestoda has necessitated a grouping based almost entirely on adult morphology. In recent years sufficient data have been gathered on the development of the fish cestodes to justify pointing out certain apparent affinities.

By the discovery of the life-history of *Diphyllobothrium latum* Janicki and Rosen (1917) were able to indicate more fully the relationship between the Digenea and the Bothriocephalids which was first suggested by Leuckart (1886). This is shown by the following points:

1. Similarity of the eggs
2. Existence of a uterine pore
3. Structure of the larvae
4. Two intermediate hosts
5. Resemblance between the miracidium and coracidium
6. Resemblance between the cercaria and the procercoid

On the basis of the points just enumerated, *Diphyllobothrium latum*, *Triaenophorus nodulosus* and *Ligula simplicissima* show a clear affinity to the Digenea. The development of *Abothrium infundibuliforme* as described by Rosen (1918) differs from the three Bothriocephalids just mentioned in respect to the fifth point. Although the egg of *A. infundibuliforme* goes through the process of hatching, it does not give rise to a ciliated larva or coracidium. In this respect it is further removed from the Digenea than the other Bothriocephalids whose life-cycles are known.

Using the points enumerated above as criteria of the relationship between Bothriocephalids and Proteocephalids, the first variation from the usual Bothriocephalid condition if found in *Abothrium infundibuliforme;* the eggs of which show an intermediate position. Since the eggs of the last-named species contain a fully formed oncosphere when extruded from the uterus, they resemble the eggs of the Proteocephalids; but since the eggs of *A. infundibuliforme* give rise to unciliated larvae, they differ from the usual Bothriocephalid condition. Except for the first and

fifth points there is substantial agreement between *Corallobothrium fimbriatum* and the Bothriocephalids. *Proteocephalus percae* agrees on the second, third, and sixth points, but *P. filicollis* and *P. torulosus* differ in all points except the second and third. Therefore, starting with a typical Bothriocephalid such as *Diphyllobothrium latum*, there is a striking series of transitions in arriving at the typical Proteocephalid condition.

The first variation is found in *Abothrium infundibuliforme;* whose larva is unciliated. Next comes *Corallobothrium fimbriatum*, which varies from the former only in the type of egg. Then *Proteocephalus percae* follows, varying from *C. fimbriatum* in the rather rudimentary condition of the cercomer. Finally, in *Proteocepalus filicollis* and *P. torulosus* a condition is reached which differs from *P. percae* in that no cercomer is reported and thereby the resemblance of its procercoid to the cercaria is lost.

On the basis of the scolex, Fritsch (1886) suggested that *Corallobothrium solidum* represented a connecting link between the Bothriocephalids and the Taenias. In the light of the knowledge of the development of the two groups there is much to support his suggestion. La Rue (1914), after a thorough study of the species of the Proteocephalidae, found them closely related morphologically to the Tetraphyllidea. However, in their development the Proteocephalids show a close affinity to the Pseudophyllidea.

SUMMARY

1. An intensive study has been made of two new species of Corallobothrium. Both species are parasitic in *Ictalurus punctatus*, *Ameiurus melas*, and *Leptops olivaris*. Woodland's proposal (1925) to delete the genus Corallobothrium has not been accepted. The genus has been retained and the two new species have been designated as *Corallobothrium giganteum* and *C. fimbriatum*. A description is given of the adult anatomy of each parasite. The scolex of *C. giganteum* is subject to wide variation. Amphitypy occurs in the arrangement of the interovarial organs of both species. A new role has been suggested for the excretory system.

2. Particular attention has been paid to the degree of infection and seasonal occurrence of these cestodes in *Ictalurus punctatus*. Among 130 adults of this species nearly 70 per cent harbored one or the other of these cestodes or both. The adult parasites occurred only from spring to fall but the plerocercoid stage was present in the final host throughout the year.

3. The life-cycle of each cestode was studied experimentally. Infection was produced in *Cyclops serrulatus* and *C. prasinus* by feeding eggs of *Corallobothrium giganteum*. Positive results were obtained by feeding the eggs of *C. fimbriatum* to *Cyclops bicuspidatus, C. serrulatus*

and *C. prasinus*. The complete development of both parasites in the first intermediate host has been described. The procercoid of *Corallobothrium giganteum* reached maturity in the Cyclops by the twelfth day after the Cyclops had been exposed to the eggs. The development of the procercoid of *Corallobothrium fimbriatum* required from 12 to 14 days.

4. Observations on the feeding habits of Cyclops reveal that organic debris and cercaria are eaten and that protozoa are consumed in large numbers.

5. Cyclops infected with mature procercoids of *Corallobothrium fimbriatum* were fed to minnows (*Notropis blennius*). Larvae were recovered from the body-cavity of the minnows 3 days after feeding. Sections of an infected minnow showed the presence of the larvae in the intestine, within the coelom, and in the musculature.

6. *Ictalurus punctatus* measuring from 2 to 3 inches in length were found to harbor adult *Corallobothrium fimbriatum*.

7. Cyclops infected with the procercoids of *Corallobothrium fimbriatum* were fed to minnows. The minnows were fed to *Ameiurus melas* and the larvae of *Corallobothrium fimbriatum* were recovered from the intestine of *A. melas*.

8. The evidence indicates that catfish may be infected with *Corallobothrium fimbriatum* either by ingesting infected Cyclops or by feeding on infected minnows.

9. A comparison of Bothriocephalid and Proteocephalid development indicates a close relationship between the two groups.

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EXPLANATION OF PLATES

All figures, except 39 and 41, were drawn with the aid of the camera lucida. The value of the scale projected is indicated in the explanation of each plate. The following abbreviations are used:

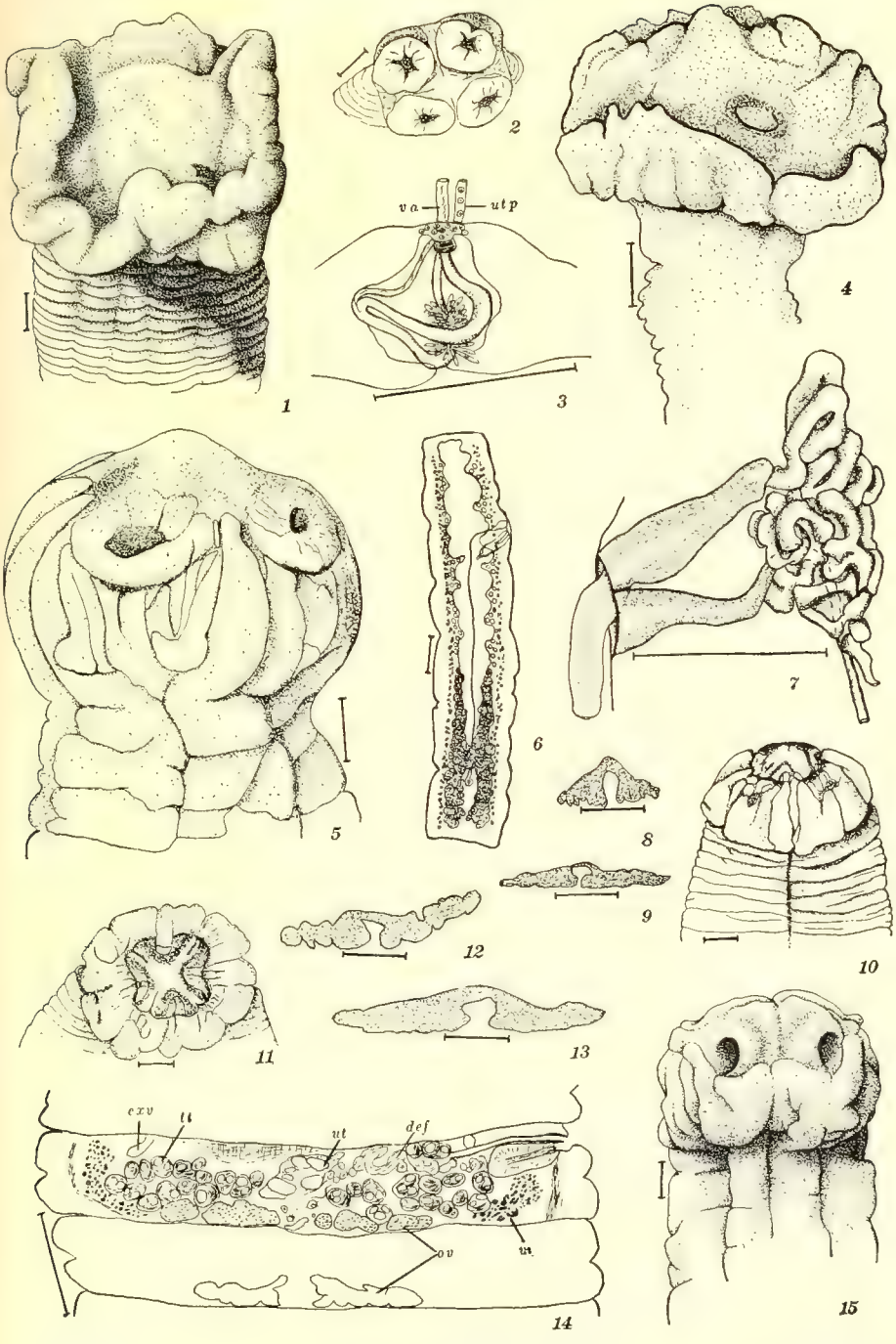
cip	cirrus-pouch	*ooc*	oocapt
dj	ductus ejaculatorius	*rs*	receptaculum seminis
def	vas deferens	*sm*	sphincter muscle
exd	excretory vessel, dorsal	*tt*	testes
exv	excretory vessel, ventral	*ut*	uterus
fs	foramina secondaria	*utl*	lateral uterine pouches
ml	longitudinal muscles	*utp*	uterine passage
mr	muscle rhomboid	*utvp*	ventral uterine pore
nl	lateral nerve	*va*	vagina
nr	nerve ring	*val*	lower vagina
od	oviduct	*vi*	vitellaria
oot	ootype	*vid*	vitelline ducts
ov	ovary	*vidc*	vitelline duct, common
		vir	vitelline reservoir

PLATE I

EXPLANATION OF PLATE I

The value of the scale projected on each figure equals 0.3 mm.

FIG. 1. *Corallobothrium fimbriatum*, scolex of adult, toto.
FIG. 2. *C. giganteum*, apical view of scolex.
FIG. 3. *C. fimbriatum*, organs of interovarial space, toto-mount. Vitelline ducts are not shown.
FIG. 4. *C. fimbriatum*, scolex of adult, toto, more expanded than fig. 1.
FIG. 5. *C. giganteum* scolex, showing apical prominence.
FIG. 6. *C. giganteum*, fully extended proglottid from near posterior end.
FIG. 7. *C. giganteum*, protruded cirrus, cirrus-pouch, vagina and vas deferens, toto.
FIG. 8. *C. fimbriatum*, ovary of immature proglottid, toto.
FIG. 9. *C. fimbriatum*, ovary of mature proglottid in same chain as fig. 8.
FIG. 10. *C. giganteum*, dorsal view of the scolex, much contracted, toto.
FIG. 11. *C. giganteum*, apical view of the same scolex as in fig. 10.
FIG. 12. *C. fimbriatum*, ovary of immature proglottid, toto.
FIG. 13. *C. fimbriatum*, ovary of mature proglottid in same chain as fig. 12.
FIG. 14. *C. fimbriatum*, frontal section of immature segment.
FIG. 15. *C. giganteum*, expanded scolex, toto.



1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

PLATE II

EXPLANATION OF PLATE II

The value of the scale projected on each figure equals 0.3 mm. except fig. 24, on which it equals 0.1 mm.

FIG. 16. *Corallobothrium giganteum*, frontal section of contracted scolex showing excretory vessels much reduced in apex.

FIG. 17. *C. giganteum*, cirrus fully protruded, drawn from living specimen.

FIG. 18. *C. giganteum*, cross-section near apices of suckers, showing sphincter about suckers and muscle fibers connecting each pair of suckers.

FIG. 19. *C. fimbriatum*, sagittal section of much contracted scolex.

FIG. 20. *C. giganteum*, cross-section at level of cirrus-pouch.

FIG. 21. *C. giganteum*, frontal section of expanded scolex showing distended excretory vessel in apex.

FIG. 22. *C. fimbriatum*, frontal section of expanded scolex.

FIG. 23. *C. giganteum*, fully expanded ovary and associated organs, toto.

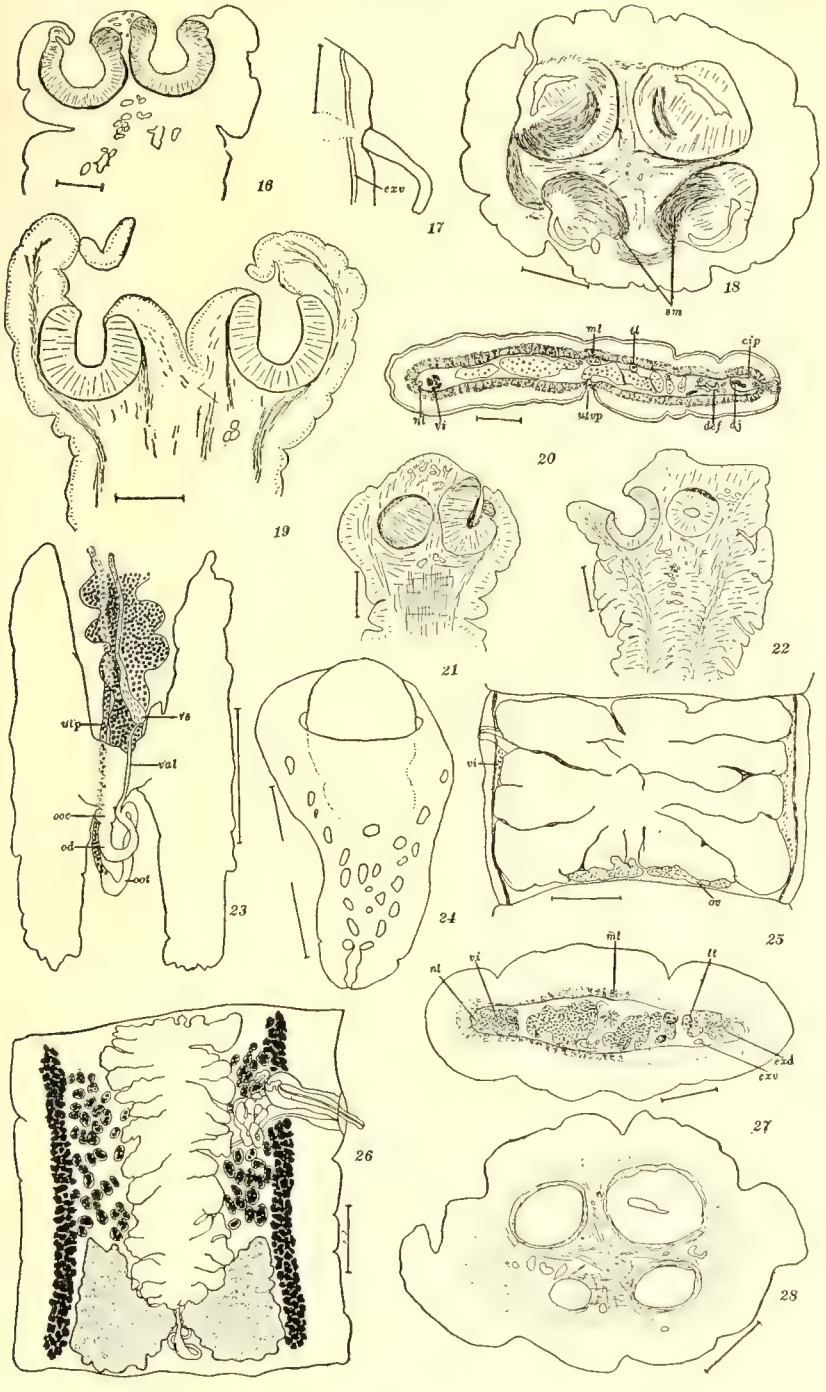
FIG. 24. *C. giganteum*, procercoid showing scolex partially protruded.

FIG. 25. *C. fimbriatum*, ripe proglottid, toto.

FIG. 26. *C. giganteum*, mature proglottid.

Fig. 27. *C. fimbriatum*, cross-section.

FIG. 28. *C. giganteum*, cross-section near posterior limit of suckers showing part of muscle star.



16 17 18 19 20 21 22 23 24 25 26 27 28

PLATE III

EXPLANATION OF PLATE III

The value of the scale projected on each figure equals 0.3 mm. except on figs. 39, 40 and 41, on which it equals 0.03 mm.

FIG. 29. *Corallobothrium fimbriatum*, frontal section of mature proglottid.

FIG. 30. *C. giganteum*, frontal section of scolex contracted as in fig. 10.

FIG. 31. *C. fimbriatum*, cross-section showing extent of uterus.

FIG. 32. *C. fimbriatum*, frontal section of dorsal region of mature proglottid.

FIG. 33. *C. giganteum*, frontal section of an expanded scolex showing the sphincter muscle of the suckers as a knob-like structure.

FIG. 34. *C. giganteum*, drawing made from three frontal sections. The proglottids shown here are three segments posterior to those shown in fig. 38.

FIG. 35. *C. giganteum*, cross-section through scolex near apices of suckers.

FIG. 36. *C. fimbriatum*, frontal section of vagina and protruded cirrus and cirrus-pouch.

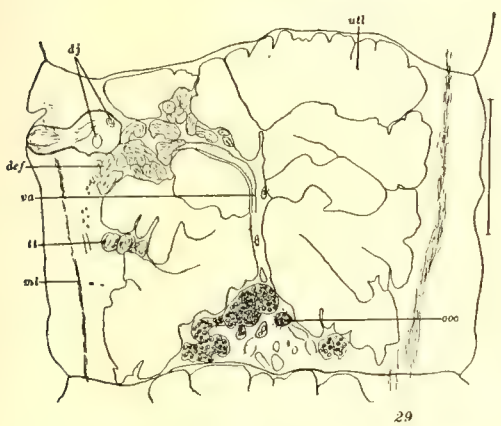
FIG. 37. *C. giganteum*, frontal section of contracted scolex, sphincter of sucker shaded.

FIG. 38. *C. giganteum*, drawn from three frontal sections. The excretory vessels are much less distended than those shown in fig. 34.

FIG. 39. *C. giganteum*, reconstruction of interovarial organs.

FIG. 40. *C. giganteum*, cross-section of dorsal excretory vessel.

FIG. 41. *C. fimbriatum*, reconstruction of interovarial organs.



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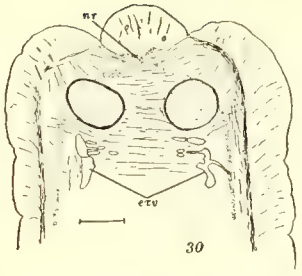

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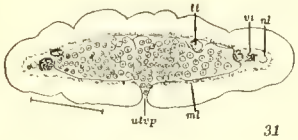

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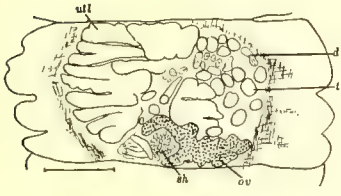

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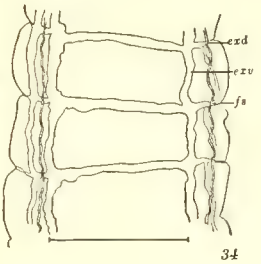

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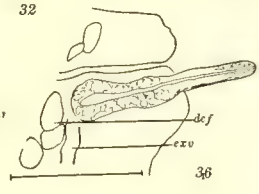

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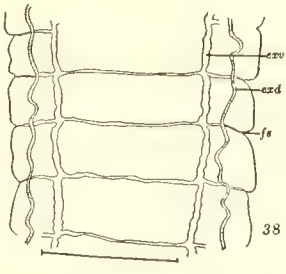

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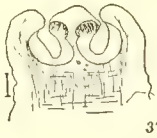

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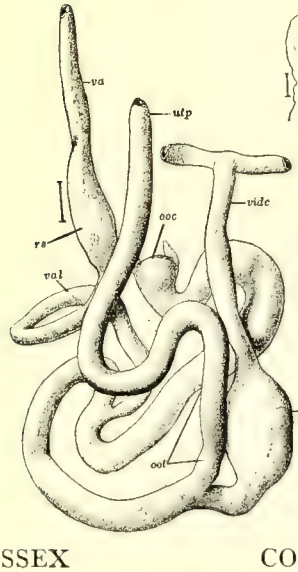

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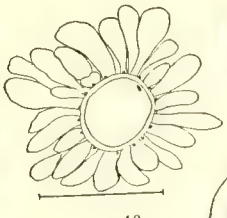

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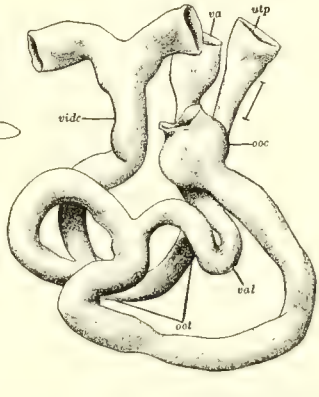

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PLATE IV

EXPLANATION OF PLATE IV

The value of the scale projected on each figure equals 0.03 mm. except on figs. 47 and 51, on which it equals 0.3 mm.

FIG. 42. *Corallobothrium fimbriatum*, mature egg. The funnel-like cavities at each pole are indicated.

FIGS. 43 and 46. *C. fimbriatum*, mature eggs in which the middle membrane is ruptured.

FIGS. 44 and 45. *C. fimbriatum*, oncosphere 10 minutes after being removed from the body-cavity of the Cyclops.

FIG. 47. *Cyclops bicuspidatus*, containing 8 *C. fimbriatum* larvae 3 days after feeding of eggs.

FIG. 48. *C. fimbriatum*, larva removed from Cyclops 3 days after feeding of eggs.

FIGS. 49 and 50. *C. giganteum*, mature eggs.

FIG. 51. *Cyclops bicuspidatus*, which contained 18 *C. fimbriatum* larvae 6 days after feeding of eggs.

FIG. 52. *C. giganteum*, tracing of oncosphere seen in the body-cavity of Cyclops 8 hours after feeding of eggs.

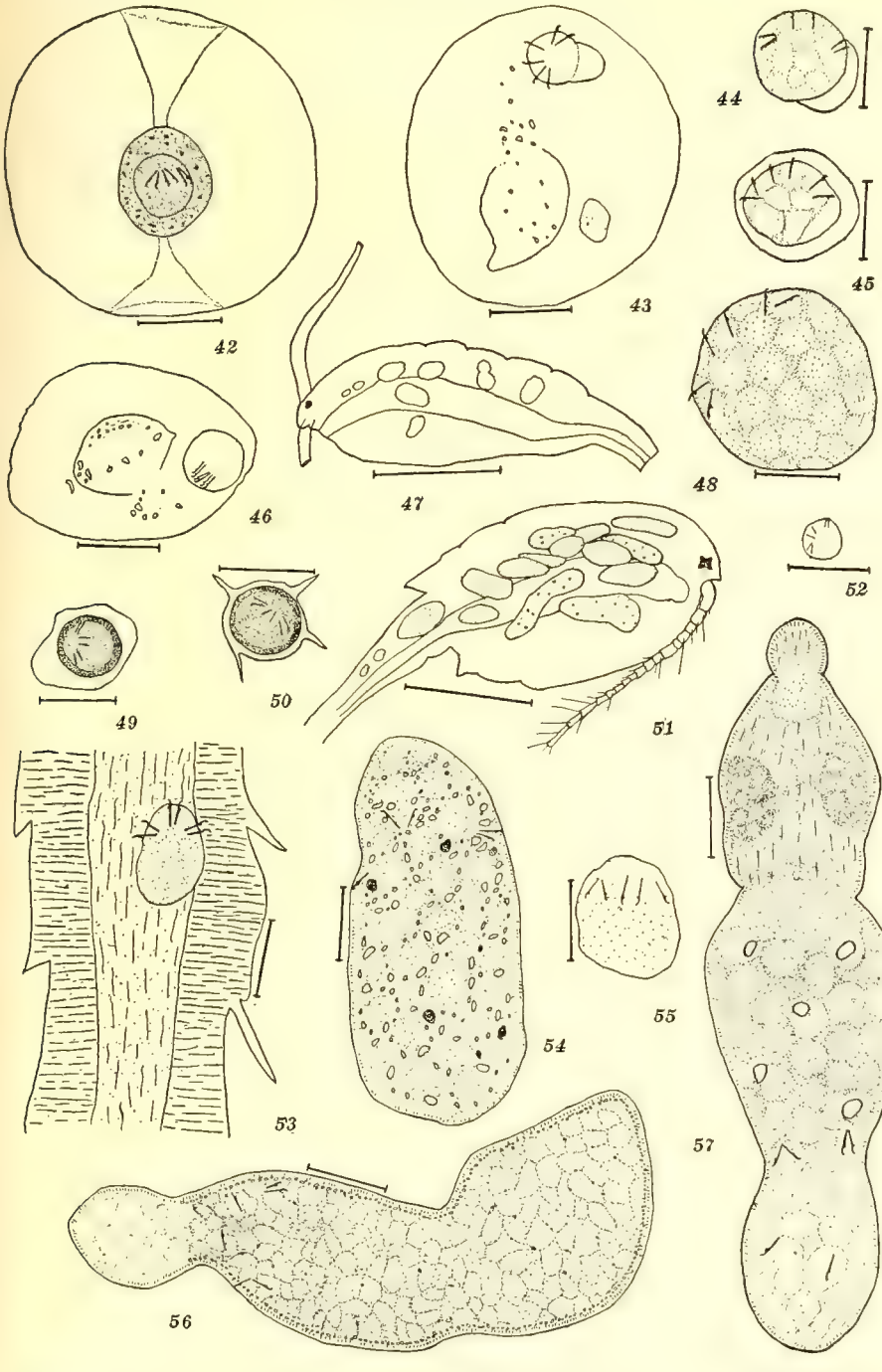
FIG. 53. *C. fimbriatum*, larva seen in abdomen of Cyclops 24 hours after feeding of eggs.

FIG. 54. *C. fimbriatum*, 4-day old larva.

FIG. 55. *C. fimbriatum*, 36-hour larva as seen through body wall of Cyclops.

FIG. 56. *C. fimbriatum*, larva about 10 days old.

FIG. 57. *C. fimbriatum*, larva from 10–11 days old.



ESSEX CORALLOBOTHRIUM PLATE IV

PLATE V

EXPLANATION OF PLATE V

The value of the scale projected on each figure equals 0.05 mm. except on figs. 62, 66, 67 and 69, on which it equals 0.2 mm.

FIG. 58. *Corallobothrium fimbriatum*, procercoid 12–13 days old with the bladder appendage still attached.

FIG. 59. Plerocercoid taken from intestine of *I. punctatus*.

FIG. 60. *C. fimbriatum*, larva somewhat contracted taken from body-cavity of *Notropis blennius* to which infected Cyclops had been fed.

FIGS. 61 and 63. *C. giganteum*, forms found in Cyclops which also contained procercoids as shown in fig. 68.

FIG. 62. *C. fimbriatum*, very young plerocercoid.

FIG. 64a, b, c, etc. *C. giganteum*, procercoid, outlines indicate shapes assumed before evagination of scolex.

FIG. 65. *C. fimbriatum*, cross-section of *N. blennius* intestine with larva outside of intestinal wall.

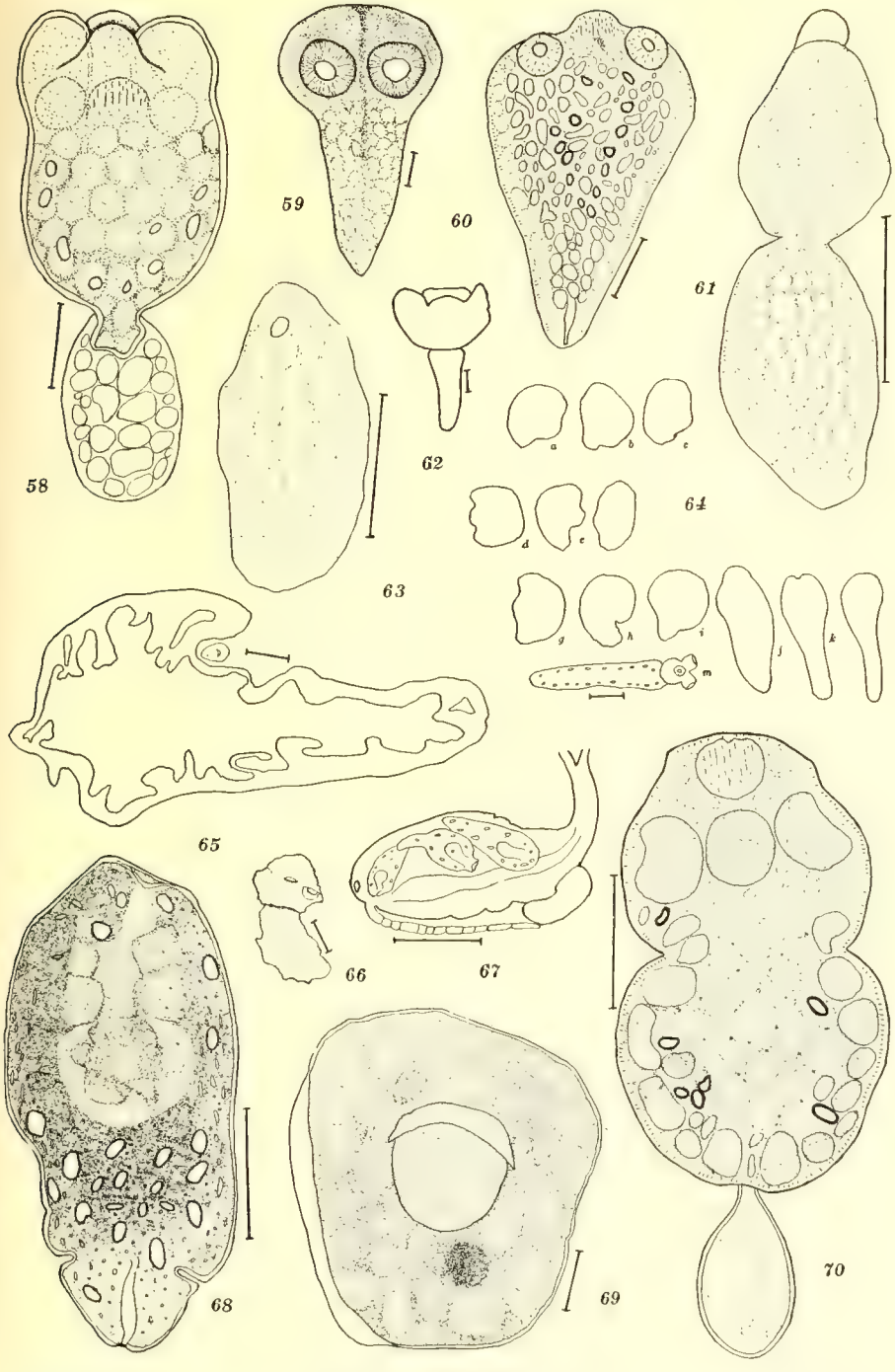
FIG. 66. *C. giganteum*, procercoid with scolex evaginated, from preserved material.

FIG. 67. *Cyclops serrulatus*, containing 3 procercoids of *C. giganteum*.

FIG. 68. *C. giganteum*, mature procercoid.

FIG. 69. *C. fimbriatum*, a much enlarged drawing of larva shown in fig. 65.

FIG. 70. *C. giganteum*, larva from 8–10 days old.



ESSEX CORALLOBOTHRIUM PLATE V